Deep-Water Incised Valley Deposits at the Ediacaran-Cambrian Boundary in Southern Namibia Contain Abundant Treptichnus Pedum

DEEP-WATER INCISED VALLEY DEPOSITS AT THE EDIACARAN-CAMBRIAN BOUNDARY IN SOUTHERN NAMIBIA CONTAIN ABUNDANT *TREPTICHNUS PEDUM*

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ABSTRACT

Valley-filling deposits of the Nama Group, southern Namibia, record two episodes of erosional downcutting and backfill, developed close together in time near the Ediacaran-Cambrian boundary. Geochronological constraints indicate that the older valley fill began 539.4±1 Ma or later; the younger of these deposits contains unusually well preserved populations of the basal Cambrian trace fossil *Treptichnus pedum*. Facies analysis shows that *T. pedum* is closely linked to a nearshore sandstone deposit, indicating a close environmental or taphonomic connection to very shallow, mud-draped sandy seafloor swept by tidal currents. Facies restriction may limit the biostratigraphic potential of *T. pedum* in Namibia and elsewhere, but it also illuminates functional and ecological interpretation. The *T. pedum* tracemaker was a motile bilaterian animal that lived below the sediment-water interface—propelling itself forward in upward curving projections that breached the sediment surface. The *T. pedum* animal, therefore, lived infaunally, perhaps to avoid predation, surfacing regularly to feed and take in oxygen. Alternatively, the *T. pedum* animal may have been a deposit feeder that surfaced largely for purposes of gas exchange, an interpretation that has some support in the observed association of *T. pedum* with mud drapes. *Treptichnus pedum* provides our oldest record of animals that combined anatomical and behavioral complexity. Insights from comparative biology suggest that basal Cambrian *T. pedum* animals already possessed the anatomical, neurological, and genetic complexity needed to enable the body plan and behavioral diversification recorded by younger Cambrian fossils.

INTRODUCTION

The trace fossil *Treptichnus pedum* is widely recognized for its role in marking the beginning of the Cambrian Period in stratigraphic successions throughout the world. In the global stratotype section in Newfoundland, the initial boundary of the Cambrian Period is defined by a point placed with specific reference to the first appearance of *T. pedum* (Narbonne et al., 1987; Brasier et al., 1994), a point also marked by a distinct change in lithology (Myrow and Hiscott, 1991, 1993; Myrow, 1992). The degree to which the first stratigraphic occurrence of *T. pedum* reflects its first evolutionary appearance—and, therefore, the degree to which global first appearances of *T. pedum* can be correlated to the boundary stratotype—depends on both its environmental distribution and facies development within basins (e.g. Gehling et al. 2001). To date, sedimentological insights into the environmental distribution of *T. pedum* remain limited, sustaining a level of uncertainty regarding the biostratigraphic resolution of regional first appearances. At the same time, greater understanding of the facies distribution of *T. pedum* can aid in the biological interpretation of this key record of early animal diversification.

Ediacaran–Cambrian sections in Namibia have become a focus for studies of biological and environmental evolution because of the rare colocation of ash beds suitable for radiometric dating, several hundred meters of intercalated carbonates for stable isotope chemostratigraphy, abundant body fossils of canonical Ediacaran and coeval calcified fossils, and some of the earliest trace fossils that record motile feeding (Grotzinger et al., 1995). The Ediacaran-Cambrian Boundary (PCB) itself occurs within

a large erosional unconformity (Grotzinger et al., 1995), and the precise stratigraphic relationships among the earliest trace fossils, carbon isotopic excursions, and geochronologic tie points near the boundary remain unclear (Grotzinger and Miller, 2008). Investigations across the southern portion of Namibia have pointed to a number of locations where incised valleys may be found (e.g. Germs 1983, Saylor and Grotzinger 1996), and the current consensus view regarding the stratigraphic position of the PCB in Namibia is to regard the base of the incised valleys as marking the boundary, with valley fill deposits representing younger strata (Germs, 1983, Gresse, 1993, Grotzinger et al. 1995, Saylor et al. 1995, Saylor and Grotzinger, 1996, Grotzinger and Miller, 2006, Blanco et al. 2011); this perspective, however, is not universal (Geyer 2005). This study investigates a series of exposures of the incised valleys on Sonntagsbrunn Farm 105, approximately 100 km SW of Keetmanshoop, Namibia (Fig. 1).

Three-dimensional exposures of incised valleys at Sonntagsbrunn Farm 105 reveal detailed paleoenvironmental relationships for the trace fossils that define the Ediacaran-Cambrian boundary in the Newfoundland stratotype section. In Namibia, valley-filling siliciclastic sediments display a range of facies, some of which, but not all, contain spectacular occurrences of *T. pedum*. These rocks lack the penetrative strain and metamorphic overprints that effect the Global Boundary Stratotype Section and Point (GSSP) section in Newfoundland. Investigating the differential occurrence of *T. pedum* traces in these facies, thus, can provide useful insight into the taphonomy of the traces, the environmental ecology of the tracemaker, and the challenges associated with using this trace fossil as a robust marker of the PCB from region to region (Strauss et al. 1992).

GEOLOGIC SETTING

The Nama Group in southern Namibia is a 3000-meter-thick succession of mixed shallow-marine and fluvial, siliciclastic and carbonate rocks exposed across much of the southern portion of the country. This succession postdates the Marinoan glaciation and, possibly, the first appearance of *Cloudina*; the upper part contains the PCB, and thus records an interval of time from approximately 550 Ma to 535 Ma (Grotzinger and Miller, 2008). The Nama Group is divided into three units, from bottom to top: the Kuibis, Schwarzrand, and Fish River subgroups (Fig. 1). In total, the Nama Group covers over 40,000 km^2; approximately one-third of this area is represented by the middle portion of this stratigraphic package—the Ediacaran-age Schwarzrand Subgroup.

The Schwarzrand Subgroup was deposited in a foreland basin in response to crustal loading from thrust sheets as subduction occurred along the Gariep Belt (~100 km west-southwest of the field site) and farther north along the Damara Belt, south of Windhoek (Germs, 1983; Gresse, 1993; Saylor, 2003); a well-developed thrust belt occurs along the western limit of Nama Group exposures (Saylor and Grotzinger, 1996).

The Schwarzrand Subgroup consists of mixed siliciclastics and carbonates, with fine-grained siliciclastics predominating near the base of the unit. Previous work has documented the sequence stratigraphy, carbonate sedimentology, and geomorphic evolution of carbonate ramps and siliciclastic-dominated packages within the subgroup (Germs 1983, Saylor et al. 1995, Saylor and Grotzinger 1996, Saylor 2003, DiBenedetto and Grotzinger 2005; Grotzinger and Miller, 2006). Carbonate lithologies are best developed on the western margin of the basin, in the depocenter where siliciclastic input

was insufficient to fill the accommodation.

The Schwarzrand Subgroup has been divided into three formations, from bottom to top: the Nudaus, Urusis, and Nomtsas formations. The Nudaus Formation contains two sequences of shale and sandstone, with rare occurrences of enigmatic carbonaceous tubes (Cohen et al., 2009) and the Ediacaran body fossils *Pteridinium* and *Rangea* (Grotzinger et al., 1995; Narbonne et al., 1997). The overlying Urusis Formation contains two carbonate platform sequences (Huns and Spitskopf members) underlain by shelf sandstone and shale units (Nasep and Feldschuhhorn members, respectively). Urusis Formation fossils include abundant populations of the probable alga *Vendotaenia* (Cohen et al., 2009), calcified metazoans associated with microbial reefs (Grotzinger et al., 2005), Ediacaran body fossils (Narbonne et al., 1997), and rare animal traces (Jensen and Runnegar, 2005). Incised valley deposits cut into the top of the Urusis Formation and are filled in by shales, siltstones, and sandstones of the Nomtsas Formation (Germs 1983). The Urusis-Nomtsas formation boundary contains incised valleys and multiple ash beds across the southern part of Namibia (Saylor, Grotzinger and Germs, 1995). Sequential ash beds dated at 545.1±1, 543.3±1, and 539.4±1 Ma by U-Pb systematics on volcanic zircons (Grotzinger et al. 1995) are distributed throughout the Schwarzrand Subgroup and yield superior age control, compared with contemporaneous localities in Avalonia.

At Sonntagsbrunn Farm 105 (27°15'56"S, 17°37'43"E), the Nomtsas Formation incises into the upper two members of the underlying Urusis Formation, forming two discrete incised valleys (Fig. 2). These are exposed in cross-section in the walls of the present-day canyon, carved by a tributary of the Fish River. Valley fill units are superimposed on one another, and can be traced for hundreds of meters in plan view;

incised valley widths appear to be on the order of 200 m (Fig. 3). The first valley fill sequence (termed VF1) achieves greater maximum width than the second, and consists of nonfossiliferous, deep-water laminated mudstones (Figs. 4, 6). The second valley fill sequence (termed VF2) contains a wide variety of sedimentary structures indicating unidirectional currents, along with abundant trace fossils assignable to *Treptichnus pedum* (Figs. 10–15).

We measured several sections on Sonntagsbrunn Farm 105 that include VF1 and VF2, with particular focus on identifying *T. pedum*-bearing facies. Several sites with VF2 deposits contained abundant traces, and two in particular ("Visionarium" [27°16'16.89"S,17°38'18.82"E] and "Section 4" [27°16'23.02"S, 17°38'17.76"E]; see Supplemental Information for Google Maps images) were the source for most of the observations reported here. Trace fossils occur on both sides of the canyon, spread over approximately 1.5 km^2 in map view. We photographed *T. pedum* traces in cross-section and plan view using a Canon digital SLR camera. Image analysis was performed using the open-source software package ImageJ, currently maintained by the National Institutes of Health (available from: http://rsbweb.nih.gov/ij).

RESULTS

STRATIGRAPHY AND SEDIMENTOLOGY

Within the study area on Sonntagsbrunn 105, measured sections span the middle and upper portions of the Schwarzrand Subgroup and the overlying Nomtsas Formation.

Urusis Formation: Feldschuhhorn Member

Sections 1 and 8; Figures 3, 4, 6

The Feldschuhhorn Member is composed of green-gray fissile shales with iron staining. These can be distinguished from shales within the Nomtsas Formation by their variability in color (Feldschuhhorn shales weather from gray to buff) and the occurrence of tubular microfossils, described by Cohen et al. (2009). Shales are composed of finely laminated mudstones, with streaky siltstone intercalations. The shales contain rare intercalated thin sandstone beds that occasionally contain low-angle crossbedding and calcareous, concretionary cements. Massive sandstone beds are also intercalated within the shales, and range in thickness up to 10 cm. Associated tubular fossils are 1-2 mm wide, curving, flattened compressions that are pyritic in fresh exposure and rusty red on weathered surfaces (Cohen et al., 2009).

The Feldschuhhorn shales are interpreted to have formed near or below storm wave-base, based on the absence of fair-weather wave-induced structures, and only the rare appearance of low-angle lamination that probably represents small-scale hummocky cross-stratification. Interbedded, massive sandstone beds may represent deposition from hyperpycnal flows (Lamb et al., 2008). Working on Swartkloofberg 95, approximately 110 km to the west of the study area, Saylor (2003) described this environment as “storm-influenced shelf;” however, our observations from Sonntagsbrunn 105 suggest that, regionally, much of the deposition occurred largely below storm wave base (SWB) during Feldschuhhorn time.

Urusis Formation: Spitskopf Member

Section 8

A limited thickness of the lower Spitskopf Member can be seen in section 8. It consists of shale and siltstone much like those of the Feldschuhhorn Member, but grades upward into black, thin-bedded, lime mudstone interpreted as the base of the upper Spitskopf Member. The lime mudstones occur at the top of Section 8 and are visible in outcrop (Fig. 6). Younger Spitskopf strata were removed by erosion prior to the onset of Nomtsas deposition.

Westward, within Swartkloofberg 95, the Spitskopf Member contains much thicker cycles of alternating siliciclastics and stromatolitic carbonate; the lowermost carbonates units are karst-capped and their depositional environment has been interpreted as a high-energy, wave-swept shelf (Saylor, 2003). Within the study area, Spitskopf Member thicknesses never exceed 2 m, limiting our ability to correlate precisely with the thicker, western sections.

On Sonntagsbrunn 105 the upper Spitskopf Member is not present as an intact, laterally continuous unit, having been differentially eroded during VF1 and VF2 incision events. In one location (Fig. 3), however, a single large block represents collapse of the Upper Spitskopf at the top of the Valley Fill 1 sequence. This block contains carbonate strata over 5 m thick and, therefore, provides indirect evidence for a once-thicker Spitskopf Member, which was truncated by pre-Nomtsas Formation erosion.

Lower Nomtsas Formation: Valley Fill 1 (VF1)

Section 3; Figures 3, 4, 5

The lower part of the Nomtsas Formation has previously been recognized to contain an incised valley complex (Germs, 1983; Saylor et al., 1995; Saylor and Grotzinger, 1996; Saylor, 2003; Grotzinger and Miller, 2008). The facies and internal stratigraphy of this incised valley complex have not been described in detail, however. Our observations show that the previous interpretation of a single valley incision event (Saylor 2003), as observed in a western, downdip location (Swartkloofberg 95), must be modified in our eastern, updip location (Sonntagsbrunn 105) to show two distinct episodes of valley incision, described here as Valley Fill 1 and 2 (VF1 and VF2). Each valley fill sequence delineates a single depositional sequence.

The most abundant facies (>80%) in VF1 is composed of finely laminated green to grey shale along with laminated siltstone containing interbedded turbiditic sandstone and occasional carbonate beds. These deposits are observed to onlap pre-incision strata at the margins of the incised valley (Fig. 19). Shales are predominantly drab olive green in color (Fig. 4). Sandstones form thin beds, less than 10-15 cm thick, and are commonly graded and cross bedded. Evidence of soft-sediment deformation is present within more massive beds. The basal strata of VF1 contain coarse, carbonate-clast conglomerates. Clasts are subangular to subrounded and are derived from black carbonates in the underlying Spitskopf Member. These carbonate conglomerates are lenticular, onlapping the sides of the VF1 basal surface and conforming to its shape, probably due to preferential compaction of the incised valley strata. The upper part of the VF1 infill succession is everywhere truncated by the basal surface of VF2.

The basal VF1 conglomerates are matrix supported and lack any evidence of traction transport or other indicators of fluvial sediment transport. It appears, therefore,

that initial valley-fill deposits in the Sonntagsbrunn area were deeper marine in origin, similar to those observed downdip to the west in Swartkloofberg 95 (Saylor and Grotzinger, 1996).

Many incised valleys filled by marine strata show initial deposits indicative of fluvial deposition. In turn, these fluvial deposits point to downcutting and bedrock incision during base-level fall, followed by accumulation of strata during base-level rise (Allen and Posamentier, 1993). In other cases, however, especially near the shelf break, headward erosion of incised valleys may occur simply by landward propagation of channels formed by mass wasting. In the case of the Nomtsas Formation, it seems the latter scenario may provide the better explanation for the valley incision; valley-filling sediments are all of marine origin, raising the possibility that the incised valleys were not cut by a regional fluvial system. Regional mapping of facies has not revealed evidence for a shelf break (Saylor, 2003), suggesting instead a low-gradient ramp dipping away from Sonntagsbrunn toward western outcrops. The incision mechanism(s) remains ambiguous, but detailed comparison of VF1- and VF2-bounding surfaces at Sonntagsbrunn and elsewhere could clarify this ambiguity.

Within VF1, there is no evidence for such larger scale facies trends as shallowing upward, coarsening upward, or other evidence of highstand progradation. The valley fill seems to have been dominated throughout by aggradation of shale and siltstone. It is possible that coarser facies were truncated at the base of VF2. Alternatively, VF1 on Sonntagsbrun 105 may record a relatively sediment-starved environment in which proximal estuaries lacked major river input, at least in this portion of the valley network. Sediment flux would have been high enough to allow accumulation of siltstone and less

commonly, fine sandstone, but not so high as to allow advance of sand-dominated shoreface deposits.

The environment represented by the infilling strata of VF1 is regarded as subwave base, with settling from suspension of mud and silt to form the bulk of the sediment volume. Episodically, thin, fine sands were deposited along the valley floor as sediment gravity flow or hyperpycnal flood deposits, likely supplied by rivers entering in the most updip portions of the network (Lamb et al., 2008). The occasional slumping of sandstone beds suggests remobilization on the flanks of the valley.

Basal carbonate-clast conglomerates are interpreted to represent shedding from paleohighs formed of the Spitskopf Member (Figs. 3, 8). Similar conglomerates were observed at the base of the incised valley system observed downdip, at the Swatkloofberg location (Saylor and Grotzinger, 1996). Remote sensing imagery and reconnaissance traverses show a series of paleo-highs ("paleo-koppies") to the southwest of Sonntagsbrunn 105, which could be sources for carbonate conglomerates that were shed into the valleys during initial infilling. Once flooded, these highs became less susceptible to erosion, limiting the generation of carbonate detritus. *Treptichnus pedum* was not observed in any beds from VF1.

Lower Nomtsas Formation: Valley Fill 2 (VF2)

Sections 4, 5, 6, 7a, 7b, 7c; Figures 3, 4, 5, 6

The majority of the VF2 sequence, which postdates VF1, is fine-grained sandstone, siltstone, and shale. Bed thicknesses range from 0.15 to 0.7mm. Fine-grained sandstone and siltstone are laterally extensive and have parallel lamination, unidirectional current

ripples, and show evidence of sediment binding, possibly through the involvement of benthic microbial mats. Interbedded, more thickly bedded sandstone exhibits basal scour and trough cross bedding. At the base of Valley Fill 2, there is a coarse, matrix-supported, poorly sorted, carbonate-clast conglomerate with strongly lenticular geometry. Conglomerates are overlain by massive, turbiditic sandstones with axially directed paleocurrents (Fig. 9). Both conglomerates and overlying sandstones can be seen to onlap the margins of the incised valley (Fig. 19).

Fine-grained, laminated to thin-bedded sandstone also preserve trace fossils of *T. pedum*. The degree of bioturbation is highly variable, from nearly absent (ichnofabric index (ii) 1 of Droser and Bottjer, 1986) to completely bioturbated, mottled strata (ii 5).

We interpret this depositional environment as lower shoreface, just above SWB at its deepest, and tide-influenced on the basis of bidirectional paleocurrents and the presence of trough crossbedding, based on sedimentary structures, including flaser to lenticular bedding and unidirectional current ripples (Fig. 9). Fine-grained sandstone with mud drapes were probably deposited by waning flows following storm or tidal flows, as described by Saylor (2003). These mud drapes are where the majority of *T. pedum* trace fossils were found.

Upper Nomtsas Formation

Sections 1, 3, and 5; Figures 3, 4, 5, 6

A capping sandstone unit at Sonntagsbrunn comprises the final valley filling unit, overtops the intravalley highs, and forms a regionally extensive sheet deposit. The intravalley highs effectively define a transgressive ravinement surface; capping

sandstones are deposited above this surface. This sandstone is pale cream-colored, fine- to medium-grained, and defines the top of the present-day canyon walls. This sandstone contains abundant current ripples, trough cross bedding, herringbone cross bedding, and scour and tool marks (Fig. 16). Some of the beds show basal scour troughs infilled by carbonate breccias and mud-chip breccias. Sandstone beds may be amalgamated or separated by thin recessive micaceous siltstones, interpreted to have been deposited during waning currents. At the base of the Upper Nomtsas Formation there is a clast-supported, semi-stratified carbonate conglomerate interbedded with sandstones, distinguishing it from other siltstone/shale-bounded conglomerates at stratigraphically lower positions in the valley fills.

We interpret the capping sandstone to have formed in a high-energy upper shoreface regime; sheet-like bed geometry signifies unconfined, post-valley flows, but with current velocities high enough to form upper plane bed stratification. Tidal currents had a strong influence on the seafloor, as shown by the presence of herringbone crossbedding, ubiquitous trough cross bedding, and presence of multimodal paleocurrent directions (Fig. 9).

PALEONTOLOGY

Treptichnus pedum is used here in broad sense of Seilacher (2007) to include straight, sinusoidal, curved, or looping burrows constructed from upward curving segments. The cumulative effect is of a burrow with a largely uniform horizontal base, from which emanate vertical or oblique projections, each of which appears to have

communicated with the sediment surface. Recent compilations of *T. pedum* occurrences are provided by Geyer and Uchman (1995) and Vannier et al. (2010). The great majority of *Treptichnus pedum* reports are from lower Cambrian strata, with fewer but still significant occurrences from the middle and upper Cambrian and from Tremadocian age beds, and even less common reports in younger rocks. These compilations show the environment of deposition of preserving strata to range from shallow marine to deep-sea settings, with a majority in the marine deposits. Geyer (2005) interpreted *T. pedum* from the upper part of the Nama Group to have been formed by opportunistic producers under environmental stress in shallow marine habitats. MacNaughton and Narbonne (1999) documented occurrences of *T. pedum* in the Mackenzie Mountains, NW Canada, from shallow marine (interdistributary lagoons and mouth bar deposits), fine-grained quartz arenites of lower shoreface deposits, and from the offshore transition and distal shelf. In their study, the greatest diversity of trace fossils was recovered from siltstone and fine-grained quartz arenites deposited between storm and fair-weather base. As a further example, Fillion and Pickerill (1990) recorded *T. pedum* from prodelta and offshore deposits in the upper Cambrian Bell Island Group, Newfoundland.

T. pedum from the Sonntagsbrunn sections

Three-dimensional exposures and numerous occurrences of *T. pedum* burrows provide an opportunity to quantify *T. pedum* dimensions. A total of 47 length and 61 width measurements were made on burrows preserved in samples observed at the Visionarium site (Figs. 10-15). By measuring these burrows and using burrow width as a proxy for the width of the organism, we were able to estimate the organism's width as 0.5

354 ± 0.3 cm (Fig. 17). We also observed examples of 0.5 cm burrows that cut themselves
355 off (Fig. 10, 11, 12). The lengths of these cutoffs constrain the maximum length of the *T.*
356 *pedum* organism to < 6 cm.

357 Trace fossils from Sonntagsbrunn 105 provide a good sample of the
358 morphological diversity of *T. pedum*. Where the burrow is straight, the vertical segments
359 generally are aligned (Fig. 12C). In curved portions of the burrow the segments generally
360 project outwards, resulting in an appearance that has been compared to a crosier (Fig. 12-
361 a,b, 13-a,b, c). The basal communication between the vertical portions of the burrow is
362 not often preserved, resulting in the appearance of isolated pods of sediment (Fig. 12-f).
363 Examination of the full range of material shows that a large range of morphologies result
364 from taphonomic variability (Fig. 12-c,d). The vertical segments may be closely spaced,
365 truncating the preceding segment (Fig. 12-b), and thereby giving the false appearance of
366 a meniscate fill. In some cases, however, successive segments are more widely separated
367 (Fig. 13-b). There are also specimens in which the segments show a zig-zag arrangement
368 (upper part of Fig. 13-c).

369 *Treptichnus pedum* of different sizes are commonly found on the same bedding
370 plane (Fig. 12-c,e,g), though the width of the vertical elements may be exaggerated by
371 compaction (Fig. 12-g). Segment width along a single burrow does not vary in the
372 material examined.

373 The base of the burrow may show a more or less well-developed longitudinal
374 division into a wide central lobe flanked by narrower lobes. This is most strongly
375 developed on burrows that closely follow the base of a bed (Fig. 14-b,c,e,g) but is also
376 seen in material that is more clearly part of common *T. pedum* morphologies (Fig. 13-f).

The lateral lobes may show dentations (Fig. 14-b,c,g). When preserved on the upper surface of a sandstone bed, the morphology is dominated by a groove with lateral ridges with less obvious signs of probes (Fig. 15).

In the Sonntagsbrunn sections, *T. pedum* is common in heterolithic bedding of the second valley fill. Most of these burrows were made within muddy sediment drapes and filled with sandy material, either during construction of the burrow or during later sedimentation. This taphonomic mode commonly yields the best-preserved material. Other traces were at least partly made within sandy beds. The absence of *T. pedum* from the first valley fill of the Nomtsas Formation suggests that the producers of *T. pedum* did not inhabit the deeper water environment. In contrast, the absence of *T. pedum* from the high-energy sandier facies of the upper Nomtsas Formation could be because high-energy settings tend to preserve only deeper-tier biogenic structures (unlike the shallow-tier *T. pedum*). Bedding soles in this facies are dominated by erosional sedimentary structures that would have eroded *T. pedum* structures were they produced in this setting. Indeed, some slabs show what may be remnants of strongly washed-out trace fossils (Fig. 15). The depositional setting represented by the second valley fill was obviously hospitable to the producer of this trace fossil.

DISCUSSION

Biostratigraphy

A pronounced carbon isotopic anomaly (Bartley et al., 1998; Amthor et al. 2003; Maloof et al., 2010;), small shelly fossils (e.g., Missarzhevsky, 1989; Qian and Bengtson, 1989), and organic-walled microfossils (Moczydlowska, 1991) have all been used to

400 located the PCB regionally, but none of these markers are available in southeastern
401 Newfoundland, where the PCB is defined globally

402 Since the GSSP was defined, *T. pedum* has been found in beds a few meters below
403 the PCB boundary in Newfoundland (Gehling et al., 2001), and traces of comparable
404 complexity have been described from uppermost Ediacaran sandstones in Namibia
405 (Geyer and Uchman, 1995; Jensen et al., 2000; Jensen and Runnegar, 2005), reducing the
406 precision of trace-fossil-based correlations to the GSSP as a consequence of abrupt facies
407 changes in the type locality (Myrow and Hiscott, 1991; Myrow and Hiscott, 1993).

408 A greater limitation, however, may be the distribution of facies favorable for
409 development and or preservation of *T. pedum*. To date, only limited information has
410 been published on the environmental distribution of these traces. Faulting in
411 Newfoundland, which can scramble context and range constraints, and abundant
412 carbonates in Namibia (an unfavorable lithology for *T. pedum*) limit the capacity to
413 resolve this distribution in these two locations.

414 Within the Chapel Island Formation in Newfoundland, Member 1 preserves a
415 number of traces assignable to *Treptichnus* sp. and *T. pedum* in close proximity to
416 desiccation and synaeresis cracks (Gehling et al., 2001 p. 214). Whereas accepted *T.*
417 *pedum* specimens above the PCB are found within sediments described as alternating
418 fine- to-medium-grained sandstone, trace fossils below the boundary occur in alternating
419 beds of siltstone and medium-grained sandstone (Myrow, 1987; Gehling et al., 2001 fig.
420 1). Two reports of sedimentary structures within strata, including synaeresis cracks and
421 current ripples, bear on the paleoenvironmental locus of these trace fossils (Gehling et al.,
422 2001 fig. 1). As these authors reported, “Considering that there is a different facies

423 below this faulted part of the section in the top of Member 1, it cannot be excluded that *T.*
424 *pedum* ranged more than the 4.41 m below the GSSP, recorded here" (Gehling et al, 2001
425 p. 216).

426 Limited populations of treptichnids are known from a siliciclastic interval of the
427 Huns Member (Nasep Member *sensu* Germs) at Arimas Farm (Germs 1972; Jensen et al.
428 2000). These are similar to the varieties of *T. pedum* observed from the Nomtsas
429 Formation, including the presence of a three-lobed basal surface (cf. Fig. 13-e). Geyer &
430 Uchman (1995, p. 191) described material having the overall morphology of *T. pedum*
431 from the Nasep Member at Holoog Farm 106. Further discoveries or descriptions of
432 these pre-Nomtsas Formation treptichnids are needed to establish if they represent
433 preservational end members of otherwise identical trace fossils or if they record a simpler
434 morphology (Jensen et al. 2000). Additionally, the Spitskop Member of the Urusis
435 Formation has yielded the trace fossil *Streptichnus narbonnei* that is of comparable
436 complexity to *T. pedum* (Jensen and Runnegar 2005). *Treptichnus pedum* has also been
437 reported to occur in Ediacaran strata in the Vahnrhynsdorp Group of South Africa
438 (Seilacher 2007), but the age of this succession is poorly known (Aceñolaza et al. 2009).

439 PCB sections at Sonntagsbrunn Farm 105 contain two superimposed incised valley
440 deposits assigned to the Cambrian Nomtsas Formation (Fig. 3, 8). The strata in these
441 valleys contain a wide range of sedimentary facies deposited across a range of
442 environments, from just above SWB (Fig. 18-c,d) to tidally influenced sandstones and
443 shoreface sandstones (Fig. 18-e,f). Despite this, *T. pedum* trace fossils only occur within
444 the upper incised valley deposit, VF2 (Fig. 16).

445 The confined occurrence of *T. pedum* to VF2 could reflect one of two possibilities.

First, the evolution and first appearance of the *T. pedum* organism in the stratigraphic record, or second, taphonomic bias associated with nonuniform preservation of facies and environmental control on the distribution of *T. pedum* first occurrences. Several reasons support the second hypothesis over the first.

Previous workers described a somewhat limited occurrence of *Treptichnus* within the underlying Huns Member (Jensen et al. 2000). The structures described are similar in form to the trace fossils observed here, and are found in siliclastic strata with a somewhat similar depositional environment—shallow marine, with current and wave structures present); however, the complex interaction of thrust faults and incised valleys at Arimas Farm 83 complicates stratigraphic placement. If these reports are correctly located stratigraphically, then the first appearance of these organisms in southern Namibia predates the younger, but more widespread occurrences reported here. This would imply that the spectacular occurrences of *T. pedum* at Sonntagsbrunn 105 are controlled by environment and taphonomy, rather than evolutionary first appearance.

In addition, available geochronologic constraints suggest that the valley filling deposits postdate the PCB. Outcrops on Sonntagsbrunn Farm establish that there are two sequences of valley fill events, not simply one base-level drawdown event as observed at more downdip locations (e.g. Swartkloofberg: Grotzinger et al., 1995; Saylor and Grotzinger, 1996). The younger VF2 event was of lower magnitude than the VF1 event, and thus its downdip equivalent may be represented by an influx of sand, for example, into the VF1 system, rather than rejuvenation of the valley system in that location. Other models of depositional dip variations predict this in incised valley systems (Zaitlin et al., 1994; Talling, 1998).

Views from near Section 5 (Figs. 3, 5, 6) illustrate Valley Fill 2 incising into shale and siltstone of Valley Fill 1 (Fig.s 20, 21). The amount of time elapsed between these valley-filling events is unknown, but strata truncated by the incised valley fill also likely predate the negative carbon isotope excursion correlative with the PCB (Grotzinger et al., 1995). Furthermore, to the west of the study area, an ash bed dated to 539 Ma occurs at the base of the valley fill deposit at Swartkloofberg (Grotzinger et al., 1995). Whether the single valley fill seen in downdip locations correlates in time to VF1, VF2, or both, it strongly suggests that the first appearance of *T. pedum* at Sonntagsbrunn Farm is at most 539 Ma (Fig. 21). Therefore, it is likely that the first appearance of the trace fossil *T. pedum* significantly postdates the Ediacaran-Cambrian boundary in southern Namibia.

This leads us to favor an interpretation of taphonomic or environmental control on distribution of *T. pedum*. Given the broad range of depositional environments in the two valley fill successions preserved at Sonntagsbrunn, and the restriction of trace fossils to one particular environment, our work suggests that the organism that created the *T. pedum* traces preferred tidally influenced shallow marine environments. If correct, these observations urge caution in using the first appearance of *T. pedum* in a given locality as marker for the PCB.

This interpretation supports initial work (Grotzinger et al., 1995) in placing the PCB within the hiatus between the Schwarzrand and Fish River subgroups. This attribution is based on paleobiological, biogeochemical, and radiometric data from several continents that link the boundary to a transition from skeletons of distinctly Ediacaran aspect (e.g., *Cloudina*, *Namacalathus*) to those characteristic of the Cambrian, a diversification of small spinose acritarchs, and a pronounced negative C-isotopic

492 excursion, all dated at 542+/-1 Ma. In most sections where *T. pedum* occurs in
493 conjunction with these other markers, it appears above *Cloudina*/*Namaclathus* and within
494 or above the carbon isotopic nadir. In contrast, Geyer (2005) places the PCB in Namibia
495 lower in the section, within the Schwarzrand Subgroup, based on the occurrence of
496 treptichnid trace fossils. Boundary placement is, in fact, difficult to resolve because of all
497 the data sources used to correlate PCB successions globally, only *T. pedum*, and
498 associated trace fossils, are available in the GSSP in Newfoundland. Limited C-isotopic
499 data from organic carbon suggest that the negative C-isotopic excursion may occur above
500 the GSSP in Newfoundland (Strauss et al., 1992), but resolution of this issue awaits
501 further work.
502 In a formal sense, alternative boundary placements in Namibia are difficult to
503 confirm or refute. What available data do make clear, however, is that the first
504 appearance of treptichnids, *sensu lato*, in Namibia predates the appearance of *T. pedum* in
505 sections from Siberia, Poland, and northwestern Canada, whereas the first appearance of
506 *T. pedum sensu stricto* in Nomtsas VF2 postdates first appearances in other well-studied
507 regions—very likely by several million years. This underscores the complicating effects
508 of environmental preference and taphonomic circumstance on the use of *T. pedum* to
509 draw boundary correlations.
510
511 Paleobiology
512 Various hypotheses have been proposed for the organisms and behavior that led to
513 *Treptichnus pedum* burrows. The most common interpretation has been of deposit
514 feeding in which sediment was processed during the production of the burrow system

(e.g. Seilacher 1955; Geyer and Uchman 1995). One potential issue with this interpretation is that there is no clear evidence for sediment-manipulation, such as meniscate fill, and that the burrows appear to have been open and passively filled with sediment. An alternative proposal is that the burrow system was for protection and dwelling and that feeding took place on the sediment surface (Jensen 1997; Dzik 2005). Vannier et al. (2010) suggested that *T. pedum* implies predation or scavenging on the basis of observations of modern priapulids. Another hypothesis suggested by Seilacher (2007, p. 182) is that an undermat miner closely following a thin sand layer made *T. pedum*; he further suggested that straight varieties show a response to paleocurrents. No clear evolutionary trends in the morphology of *T. pedum* have been recorded (Seilacher 2007). Neto de Carvalho (2008), however, reporting on *T. pedum* from the deep-water Devonian Terena Formation of Portugal, suggested that a pattern of onshore-offshore displacement recorded in many traces fossils could apply also to this type of trace fossil. These traces bear great similarity to burrows that have been variously assigned to *Hormosiroidea* or *Ctenopholeus*. Fürsich et al. (2006) interpreted *Ctenopholeus kutcheri* (lower Cambrian, Jurassic) as an open burrow system that functioned to trap small motile organisms. *T. pedum* has a cosmopolitan distribution and long stratigraphic range. Over this time and space *T. pedum* must have been made by different producers and may include more than one type of behavior. Biological interpretation, therefore, might usefully be discussed on a case-by-case basis.

By definition, *T. pedum* is the earliest Cambrian animal trace fossil (Brasier et al., 1994). That similar traces may actually occur somewhat earlier in Newfoundland and Namibia only reinforces the status of *Treptichnus pedum* as the oldest evidence for

538 animals that combine morphological and behavioral complexity. There is general
539 agreement that the *T. pedum* tracemaker was a motile bilaterian animal that lived below
540 the sediment-water interface, propelling itself forward in upward curving projections that
541 breached the sediment surface (Seilacher, 1955; Seilacher and Hemleben, 1966; Geyer
542 and Uchman, 1995; Jensen, 1997; Dzik, 2005). Accepting this, *T. pedum*'s functional
543 biology might be interpreted in two distinct ways. The *T. pedum* animal might have lived
544 infaunally to avoid predation or desiccation, surfacing episodically to feed and obtain
545 oxygen. Alternatively, the animal might have been a sediment feeder that surfaced
546 regularly to exchange gases and perhaps to disperse eggs, sperm or fertilized eggs. The
547 restriction of Namibian *T. pedum* populations to environments where subaerial exposure
548 was not a chronic challenge suggests that protection from adverse physical conditions
549 was not a primary function of the burrow.

550 Priapulids, an invertebrate phylum with a prominent Cambrian fossil record, are
551 most commonly suggested as producers of this type of trace fossil. Orlowski & Zylinska
552 (1996) documented surface sculpture on Polish material of the middle and late Cambrian
553 *Treptichnus rectangularis* that they attributed to terminal spines in Cambrian priapulids.
554 On this basis, and noting points of comparison to Cambrian body fossils, Dzik (2005)
555 argued that the *T. pedum* animal was a priapulid worm, a conclusion seconded by
556 Vannier et al. (2010) on the basis of actualistic experiments. Living *Priapulis caudatus*
557 move through the sediment surface by extending their anterior proboscis, anchoring it to
558 the substrate, and then pulling the rest of the body forward. The worms change direction
559 constantly, generating a lobed trackway in which successive finger-like projections are
560 offset by ~30 degrees. The resulting track bears comparison to *T. pedum* in two

561 dimensions, although it does not have *T. pedum*'s three-dimensional complexity (Vannier
562 et al., 2010). For this reason, Vannier et al. (2010) concluded that the Cambrian *T.*
563 *pedum* animal could have been a stem group bilaterian with anatomical complexity
564 comparable to that of modern priapulids, rather than a pripaulid *per se*. While there is
565 ample data on the burrowing mechanism of modern priapulids, very little is known about
566 the type of burrows they construct. The only available data is from *Halicryptus*
567 *spinulosus*, which form relatively deep vertical burrow systems (Powilleit et al. 1994)
568 that bear little resemblance to *T. pedum*.

569 Building on the priapulid analogy, Vannier et al. (2010) interpreted the *T. pedum*
570 animal functionally as a predator on small invertebrates. Most modern priapulids prey on
571 other small animals in the sediment, but a few feed on organic debris and at least one,
572 *Maccabeus tentaculatus*, is a trap feeder, living in a tube and ensnaring unsuspecting prey
573 (Brusca and Brusca, 1990). The environmental specificity of Namibian *T. pedum* casts
574 doubt on their interpretation as foraging or trapping predators, although further analysis
575 of Sonntagsbrunn 105 material could shed more light on this problem.

576 Whether a predator, deposit feeder, or infaunal filter feeder, the *T. pedum* animal
577 must have possessed paired muscles and a hydrostatic skeleton to facilitate movement
578 through the sediment. Living priapulids exchange gases by diffusion across their
579 epidermis, but the Cambrian trace fossils hint that their tracemaker may have had anterior
580 tentacles or other appendages for gas exchange or prey capture (Fig. 14). They certainly
581 had anterior sensory and feeding organs, as well as a well-developed gut. Webster et al.
582 (2006) have argued that the slowly evolving priapulids provide our best anatomical and
583 genetic guide to ancestral ecdysozoan biology. Thus, living priapulids may provide

broad insights into *T. pedum* biology, even if the specimens of *Treptichnus pedum* do not offer specific clues to the producers' morphology. The Nomtsas Formation material offers a possible exception in the form of denticle-like protrusions on the lateral lobes in some specimens (Fig. 14-b,c,g). Although it cannot be excluded that these relate to the animals' burrowing mechanism, they could reflect differentiation along the ventro-lateral margin of the producer.

As a bilaterian animal, the producer(s) of *T. pedum* must have possessed the array of regulatory gene families common to living bilaterians. Many of the cell adhesion and signaling genes that play important roles in bilaterian development occur deeper within the opisthokont tree, even in single-celled sister groups of the metazoans (King et al., 2008; Sebè-Pedrós et al., 2010; Knoll, 2011). With that in mind, comparative genomics indicates that a great deal of gene network evolution took place along the evolutionary pathway from sponges to eumetazoans (bilaterians and cnidarians), and still more gene duplication defined the path from ancestral eumetazoans to bilaterian animals (Degnan et al., 2009; Srivastava et al., 2010). As reviewed by Erwin (2009), the earliest crown group bilaterians arguably possessed a rich array of transcription factors for developmental regulation, including seven or eight HOX genes for anterior-posterior patterning; eight or more additional ANTP-class genes including ParaHox and NK genes that further specify body organization; dorsal-ventral patterning controlled by the sog/chordin dpp/BMP2/4 system; eye formation directed by Pax6 and interacting genes; heart differentiation mediated by Nkx2.5/tinman; and miRNAs that further help to guide development. All of these gene families and more were probably present in the producer of the earliest *T. pedum*, as, by functional interpretation, were *Distalless* family genes that

607 underpin appendage formation in living bilaterians (Panganiban et al., 1997). Indeed,
608 much of this developmental toolkit was probably assembled earlier, as evidenced the
609 Ediacaran bilaterian *Kimberella*, found in 555-560 Ma rocks (Fedonkin, 2007).
610 *Treptichnus pedum*, then, reinforces the view that key genetic innovations that made
611 bilaterian diversification possible were largely in place as Cambrian time began.
612 Behaviorally, *T. pedum* is characterized by frequent angular offsets to its forward
613 and upward motion, with a directional bias that commonly leads to circular or spiral
614 meanders (Fig. 11). Functionally, such behavior would have worked to keep the *T.*
615 *pedum* animal within the narrow environmental zone in which foraging was most
616 profitable. Functional inferences suggest that *T. pedum* moved in response to two distinct
617 environmental cues – oxygen and food. The interacting behavioral responses to these
618 cues are widespread in extant organisms and have been studied extensively in the
619 experimental roundworm *Caenorhabditis elegans*. In *C. elegans*, two distinct sets of
620 sensory neurons induce the worms to move away from microenvironments with
621 suboptimum oxygen levels: so-called URX sensory neurons are activated by high
622 oxygen, whereas BAG neurons respond to low oxygen levels (both systems employ
623 signaling via cyclic guanosine monophosphate and the neurotransmitter serotonin; Chang
624 et al., 2006; Zimmer et al., 2009). Living priapulids exhibit a pronounced tolerance for
625 low oxygen levels, and O_2 would have been a persistent issue for *T. pedum* in muddy
626 sediments. Thus, there is reason to believe that the tracemakers of Nomstas *T. pedum*
627 possessed sensory neural networks broadly comparable to those in living roundworms.
628 Food cues also stimulate movement, although these can be overridden by the need
629 to maintain optimal oxygen levels (Chang et al., 2006). Notably, *C. elegans* responds to

changing food cues by forward movement, with episodic reorientation—as observed in *T. pedum*. Foraging in *C. elegans* uses interacting sensory (olfactory) and locomotory neurons, with additional neuronal circuits developing through life to enable such learned responses as food avoidance (Ha et al., 2010).

In summary, then, the *T. pedum* animal was anatomically, behaviorally and genetically sophisticated, possessing, at the very beginning of the Cambrian Period, the interacting morphological and neurological complexity needed to fuel both the body plan and behavioral diversification recorded by younger Cambrian skeletal, carbonaceous, and trace fossils.

CONCLUSIONS

Sedimentary rocks that span the Ediacaran-Cambrian boundary in southern Namibia record two episodes of valley incision and fill. The older valley fill, which includes a 539.4+/-1 Ma ash bed near its base, contains unfossiliferous, relatively deep water marine deposits. In contrast, the younger valley fill consists of lower shoreface deposits containing the trace fossil *Treptichnus pedum*. These traces are commonly used to mark the base of the Cambrian System, but there first appearance in the Nambian succession reflects sequence development, ecological preference and taphonomic circumstance, complicating the use of *T. pedum* in biostratigraphy. Excellent preservation facilitates paleobiological interpretation of *T. pedum*, suggesting that genetic, developmental and behavioral complexity inferred for younger Cambrian body fossils was in place as the period began. These complex traces underscore the view that

Cambrian diversification does not simply record an explosion of skeletons, but a true architectural and behavioral radiation that encompassed the entire animal kingdom.

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FIGURE CAPTIONS

Figure 1: Geologic map of Namibia with the study area, Sonntagsbrunn Farm 105, marked.

Figure 2: A) Local map of study area, showing location of measured sections and viewing directions of annotated photomontages (arrows). Dashed line indicates line of transect (Figures 4 and 20). Google Earth image of study area, showing location of local landmarks (roads and Sonntagsbrunn farm), measured sections and locality of extraordinarily abundant *Treptichnus pedum* traces (“Visionarium”). Numbers are latitude and longitude.

Figure 3: Annotated photomosiac of location “Trail Ridge”, showing incised valley stratigraphy. Valley Fill 1 and Valley Fill 2 cut down to the Feldschuhhorn Member in this location. From the base of the valley to the top of the cliff is approximately 150 meters. Stratigraphic thicknesses can be estimated from Figure 7.

Figure 4: Annotated photomosaic of Valley Fill 1, showing relationship between Spitskopf and Feldschuhhorn Members and overlying sheet sandstones of the Upper Nomtsas Formation. From the base of the valley to the top of the cliff is approximately 150 meters.

Figure 5: Annotated photomosaic of Valley Fill 2 stratigraphy, showing relationship between Feldschuhhorn Member, Valley Fill 2, and Upper Nomtsas Formation. From the base of the valley to the top of the cliff is approximately 150 meters.

Figure 6: Annotated photomosaic of Feldschuhhorn Member, Valley Fill 1, and Valley Fill 2 stratigraphy in relation to the upper Nomtsas Formation. Measured section 8 is through this outcrop of the Feldschuhhorn Member and contains tube-like microfossils (Cohen et al. 2009). Trace of VF1 and VF2 and contact with Feldschuhhorn Member is obscured in center of photo by rubble. From the base of the valley to the top of the cliff is approximately 150 meters.

Figure 7: Measured stratigraphic sections from Sonntagsbrunn 105. Locations are indicated in Figures 2a and 2b.

Figure 8: Key sedimentologic relationships from Sonntagsbrunn Farm area. Section numbers as in Figure 2. Y-axis scales are the same between each measured section. Note the relatively limited lateral and vertical extent of Valley Fill 2 strata.

Figure 9: Paleocurrent directions from tidally-influenced sandstones in the Nomtsas Formation. Number of measurements: 50. Note paleocurrent direction asymmetry.

Figure 10: Plate of *T. pedum* trace fossil morphology. Scale bar is cm. All images are from soles of beds.

Figure 11: Plate of *T. pedum* trace fossil morphology. Scale bar is cm. (A) Smaller traces, although less common at Sonntagsbrunn, exhibit the same morphology as the larger traces, but at 1/3 the scale--this could be a juvenile form of the organism, or an entirely different organism.

Figure 12: *Treptichnus pedum* preserved on sandstone bed soles. A-B, Specimen with curved portions in which the segments project outwards, resulting in an appearance that has been compared to a crosier. C,D, F, Specimens in which vertically oriented portions are preferential preserved. E, Close-up of small specimen in lower right portion of image C. G, Two different-sized specimens. Note, however, the thin burrow connecting vertical portions in the larger specimes, which suggests that the width of the vertical portions may have little bearing on the diameter of the producer.

Figure 13: Treptichnus pedum preserved on sandstone bed soles. A-D, Curved specimens showing differences in the spacing of vertical probes. Note zig-zag development of burrow in upper part of C. E-F, Specimens largely preserved as disjunct probes, in places showing a three-lobed basal surface.

Figure 14: *Treptichnus pedum* preserved on sandstone bed soles, with examples of specimens with a three-lobed basal surface and narrow lateral lobes with a fine transverse ornamentation. E is a close-up of central area in D. G shows burrow segments in upper part of F with a different orientation (rotated 180 degrees). Inserts in B and G are close-ups.

Figure 15: A-C- Top surface of sandstone bed covered with *Treptichnus pedum* preserved as grooves. B is a close up of top area in A. Hammer-head in A is 24 mm wide. Furrows in C are about 5 mm wide.

Figure 16: Plate of *T. pedum*-bearing strata. (A) Closeup of recessive mudstones within lower portion of Valley Fill 2. (B) Closeup of siltstones within lower portion of Valley Fill 2. C) *T. pedum*-rich unit. (D) Closeup of cross-section of *T. pedum* beds. (E) Cross-bedded, tidally-influenced siltstones with *T. pedum* trace fossils in foresets. (F) Closeup of E. Note circular cross-sections of *T. pedum* traces.

Figure 17: Histograms of *T. pedum* trace length and width. Note that with a large enough

745 sample size, there appears to be a continuous distribution of burrow widths, from
746 approximately 0.35cm to over 0.9cm, suggesting a single population with slight variation
747 in size. Mean track length is 7.49 cm, mean track width is 0.56 cm.
748
749 Figure 18: Sedimentary features and structures found on Sonntagsbrunn Farm. (A)
750 Outcrop of Feldschuhhorn Member from measured section 8. Note the white-weathering
751 shales. (B) Carbonate-clast conglomerate from Spitskopf Member. Note tabular clasts
752 suggesting minimal transport. (C) Fissile shales from Valley Fill 1 cut by medium-
753 grained siltstones of Valley Fill 2. (D) Mudstone drapes and siltstone-sandstone
754 interbeds from Valley Fill 2. Arrow indicates cross-section of *T. pedum* burrow. (E)
755 Unidirectional current ripples from upper portion of Valley Fill 2. (F) Tool marks from
756 base of bed in upper portion of Valley Fill 2.
757
758 Figure 19: Outcrop-scale onlap of valley fill deposits. (A) Onlap of Valley Fill 1 relative
759 to Feldschuhhorn Member shales, inset from Figure 3. (B) Onlap of Valley Fill 2 on
760 Valley Fill 1 shales.
761
762 Figure 20: Summary of local and regional stratigraphic relationships from Sonntagsbrunn
763 Farm. Top left: regional geologic and stratigraphic interpretation from Saylor and
764 Grotzinger (1996). Below, a transect from the southeast to the northwest of sections on
765 Sonntagsbrunn. Valley Fills 1 and 2 are interpolated between sections; where they are
766 not present in measured section, stratigraphic relationships have been interpolated using
767 outcrop photos.

Figure 21: Incised valleys on Sonntagsbrunn Farm in their regional context, modified from Germs (1985).

Supplemental Figure Captions

Figure S1: KMZ file containing GPS locations of all measured sections and key areas. (Compatible with Google Earth™)

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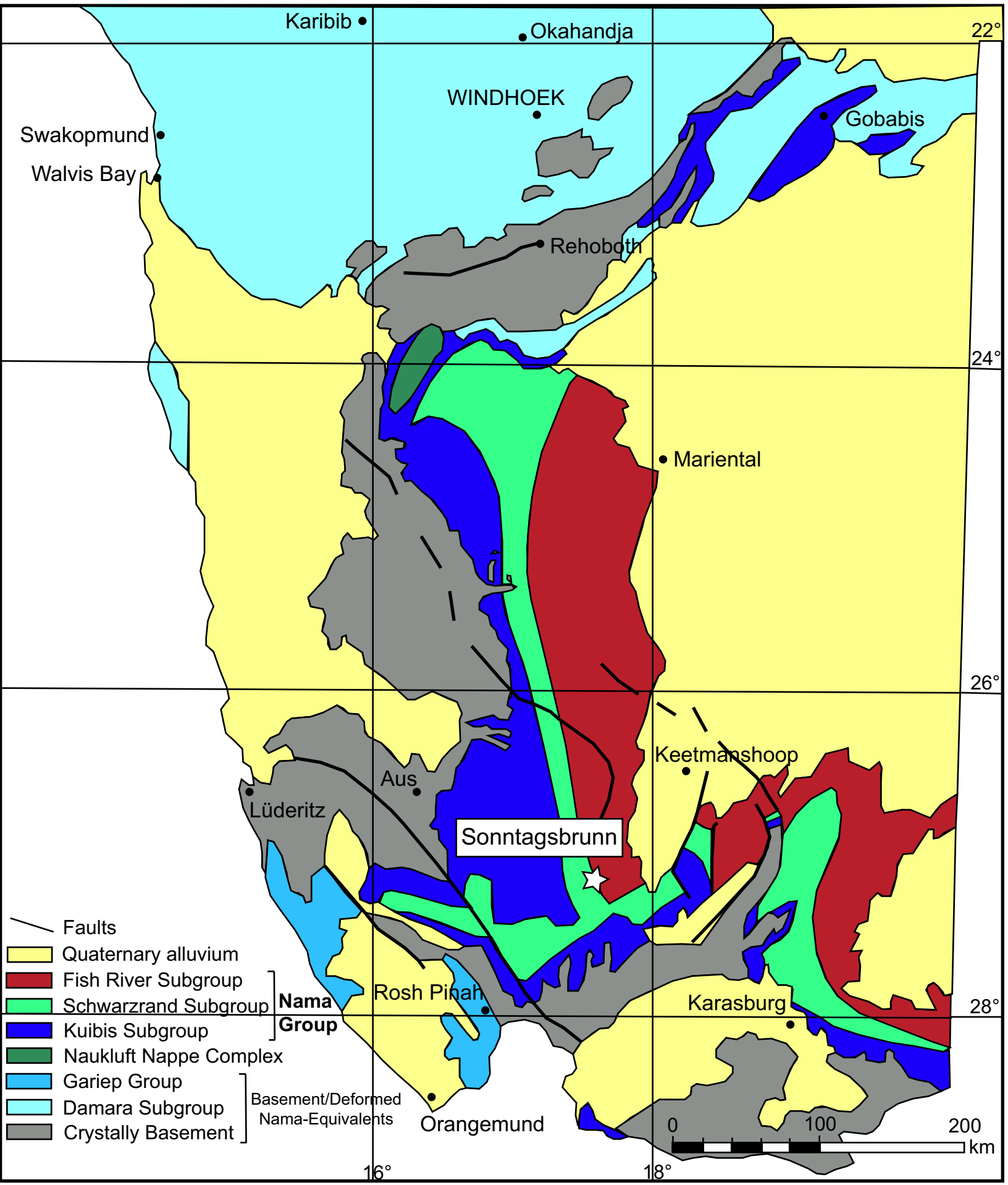
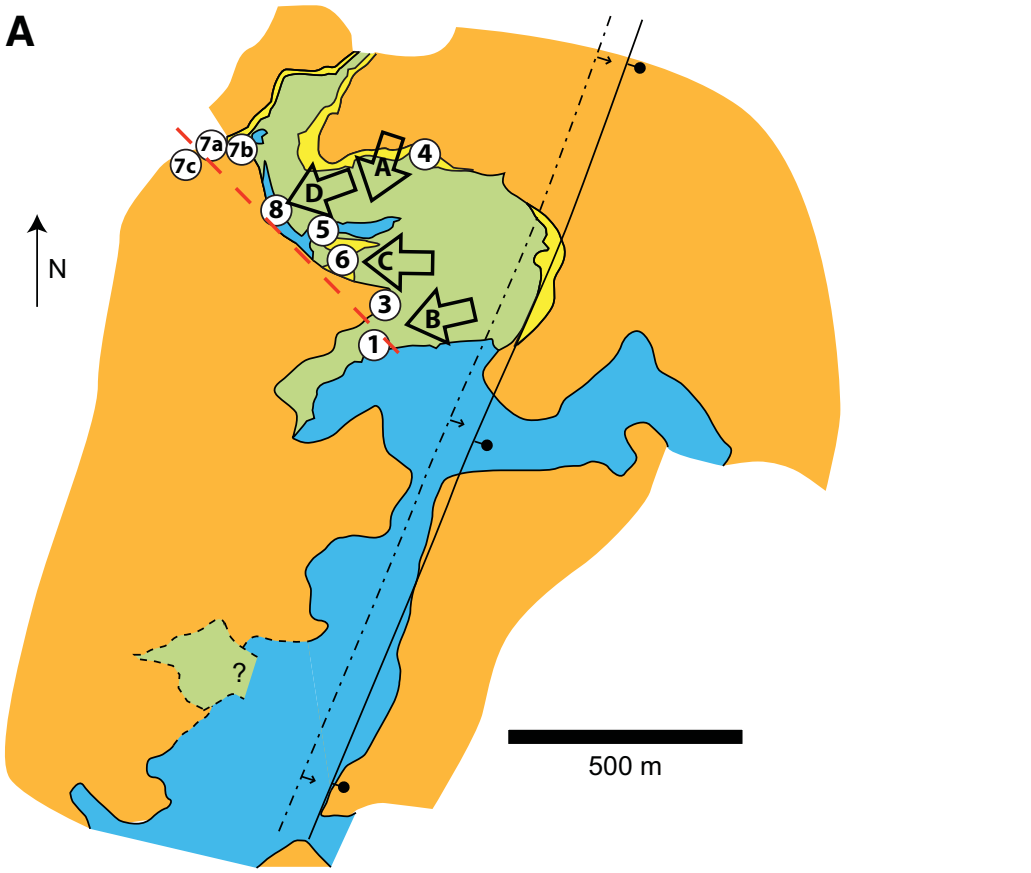

Karibib
Okahandja
22°
WINDHOEK
Gobabis
Swakopmund
Walvis Bay
Rehoboth
24°
Mariental
26°
Keetmanshoop
Aus
Lüderitz
Sonntagsbrunn
Rosh Pinah
Karasburg
28°
Orangemund
0
100
200
km
16°
18°
Faults
Quaternary alluvium
Fish River Subgroup
Schwarzrand Subgroup
Kuibis Subgroup
Nama Group
Naukluft Nappe Complex
Gariep Group
Damara Subgroup
Crystally Basement
Basement/Deformed Nama-Equivalents



Upper Nomtsas Formation (Є); rare *T. pedum*

Lower Nomtsas Formation: Valley Fill II (Є); abundant *T. pedum*

Lower Nomtsas Formation: Valley Fill I (Є); *T. pedum* rare to absent

Feldschuhhorn and Spitskopf members (pЄ); no *T. pedum*

F/H Normal fault — Homocline — — Transect

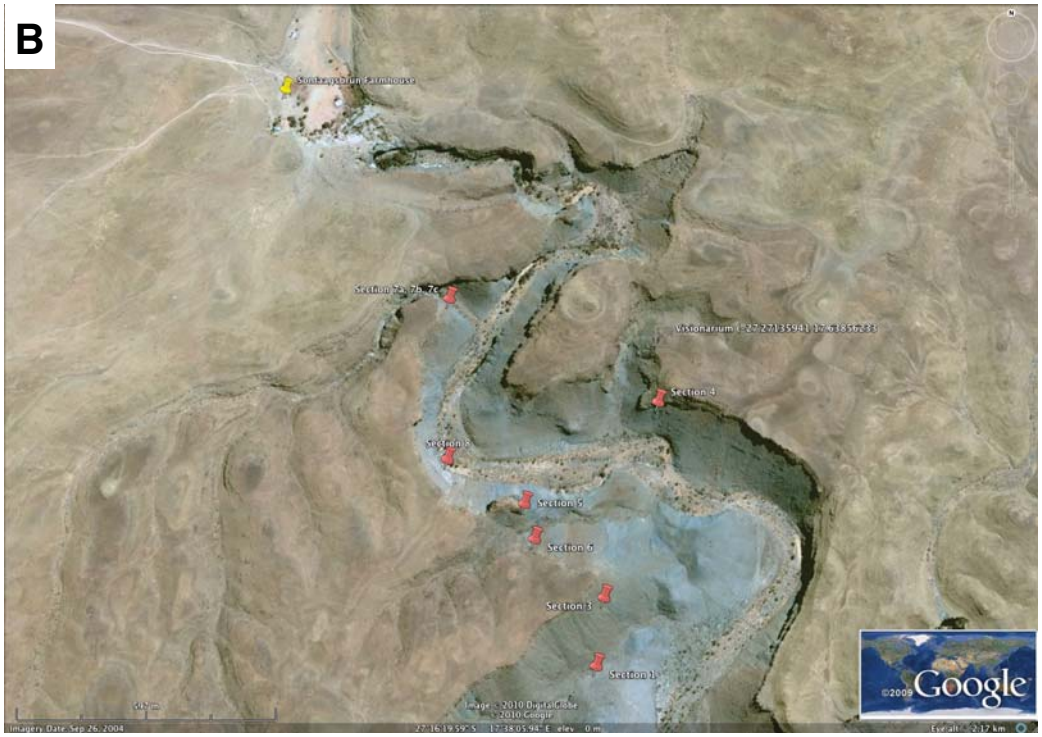
1 Measured section

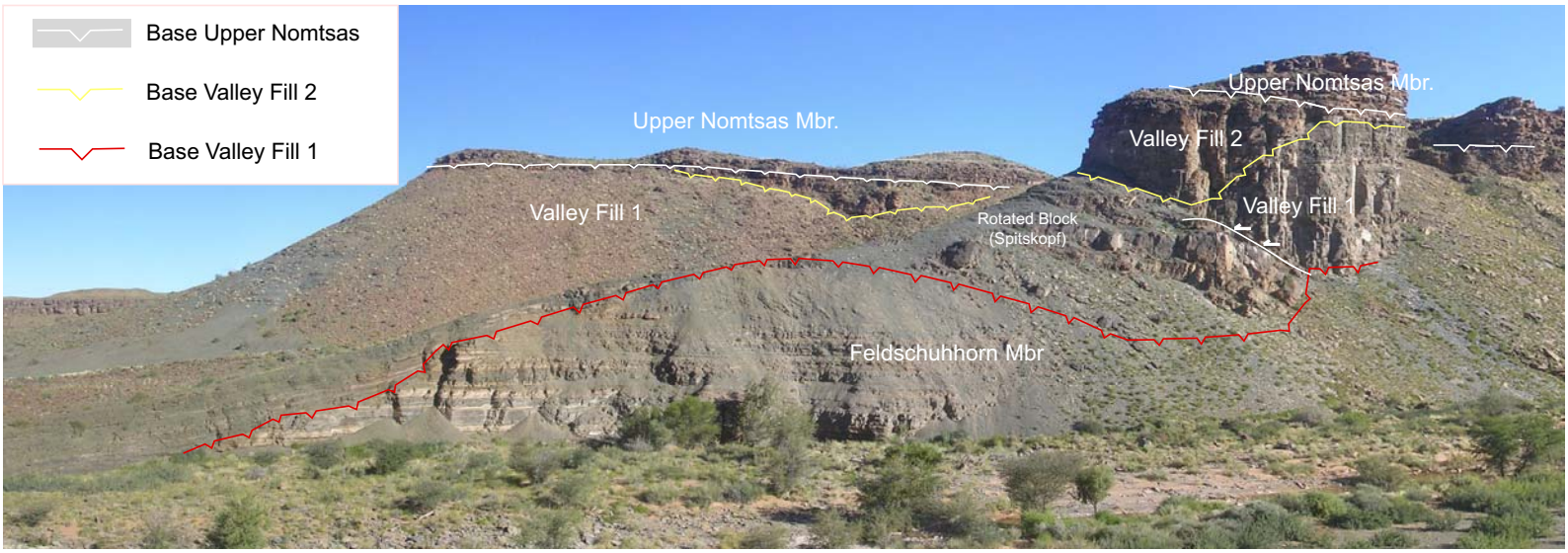
A Trail Ridge View

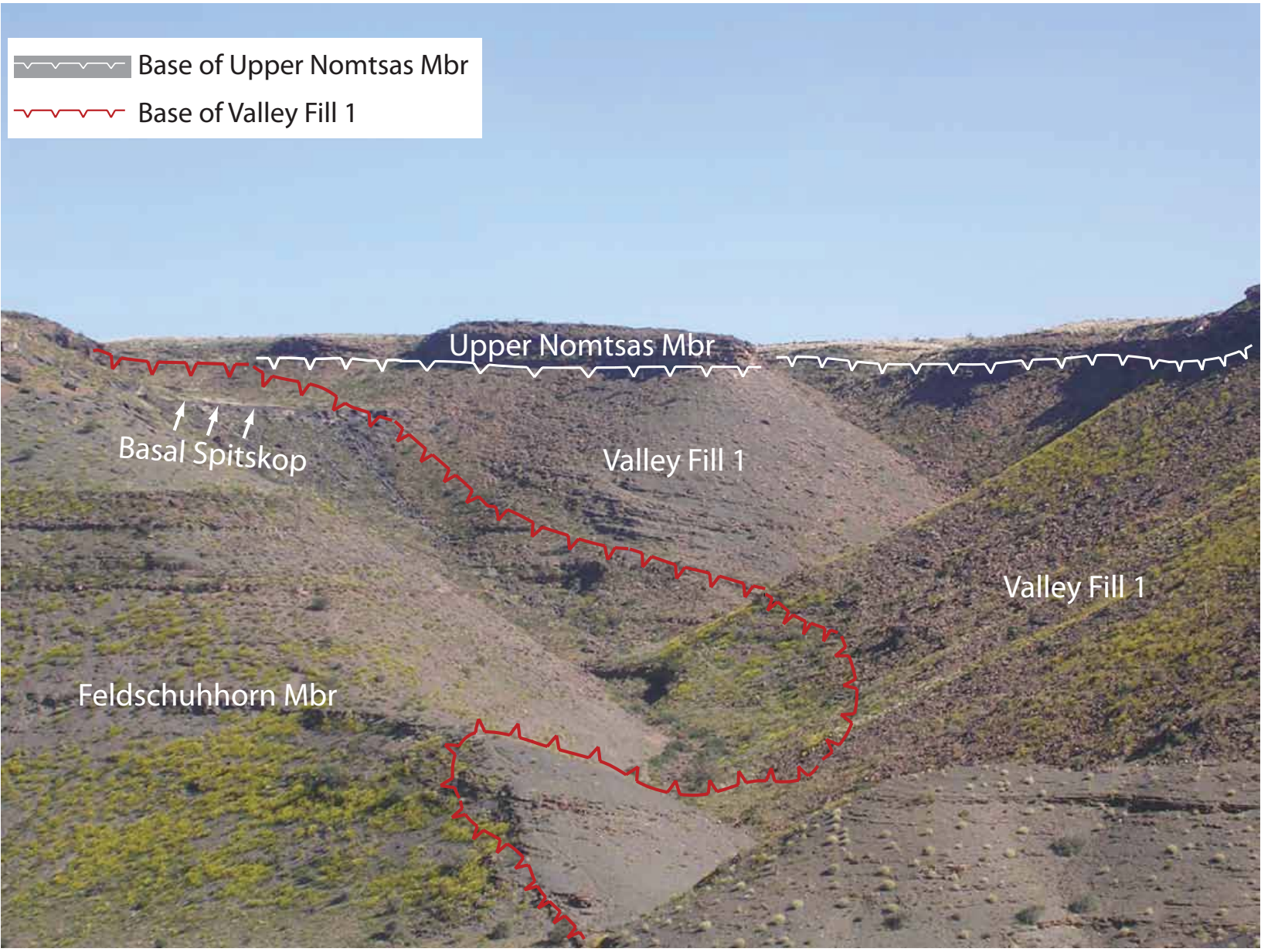
B Valley Fill 1 View

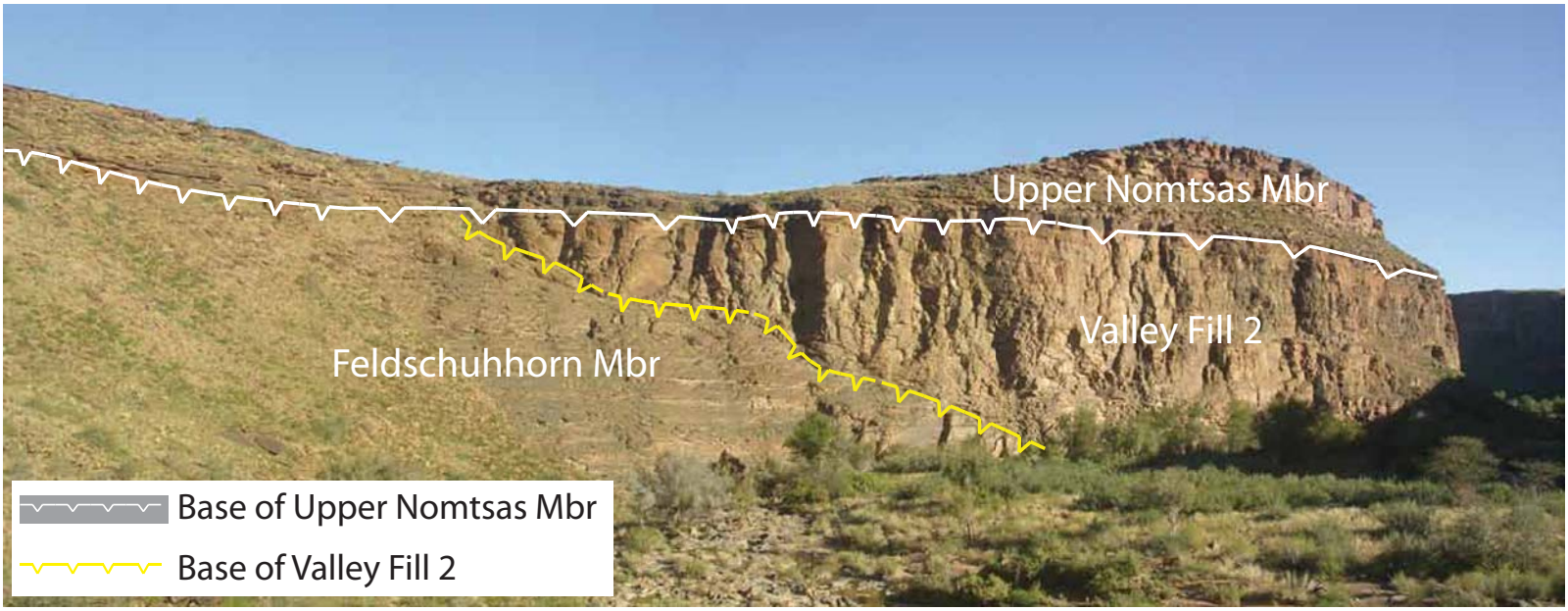
C Valley Fill 2 View

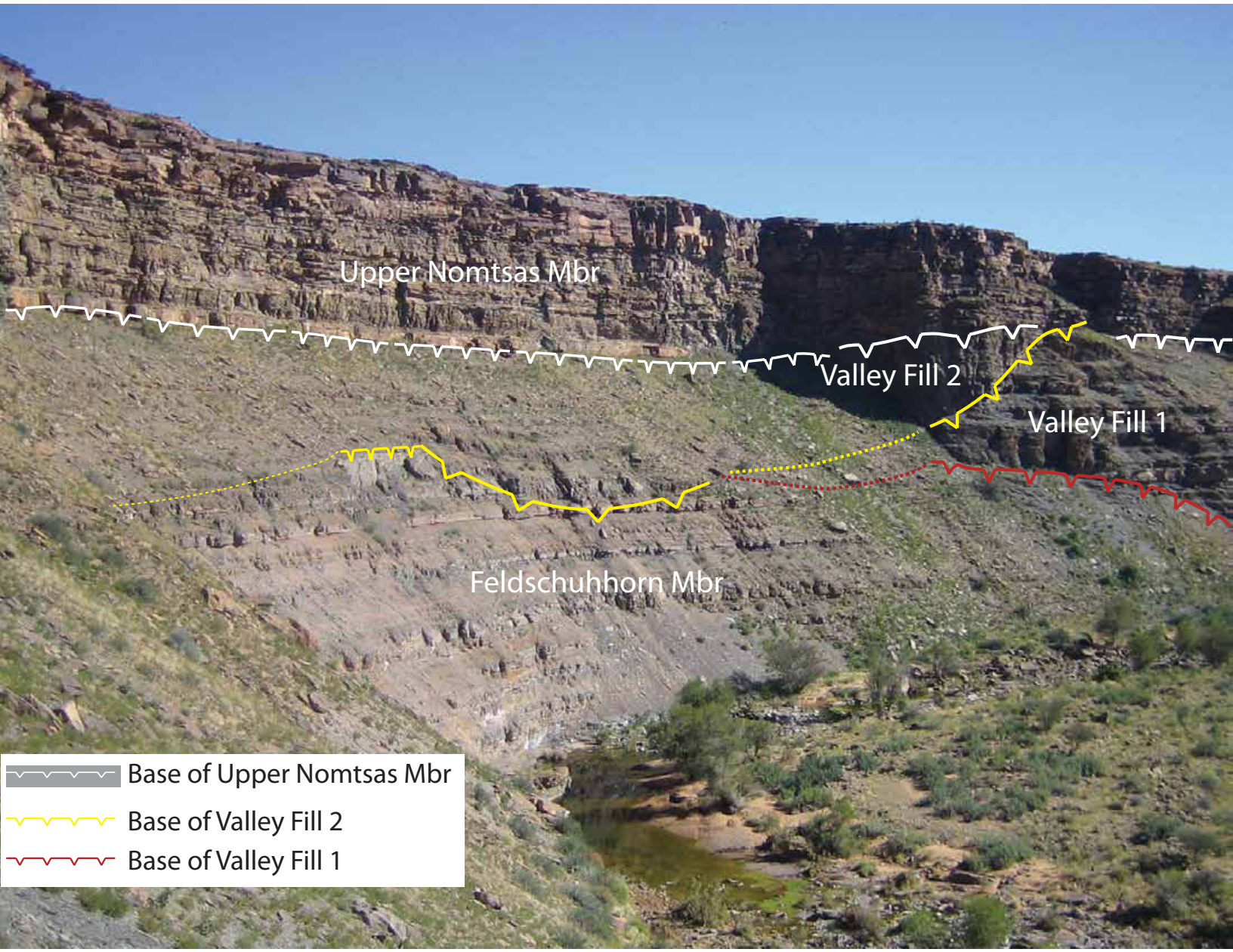
D Feldschuhhorn View

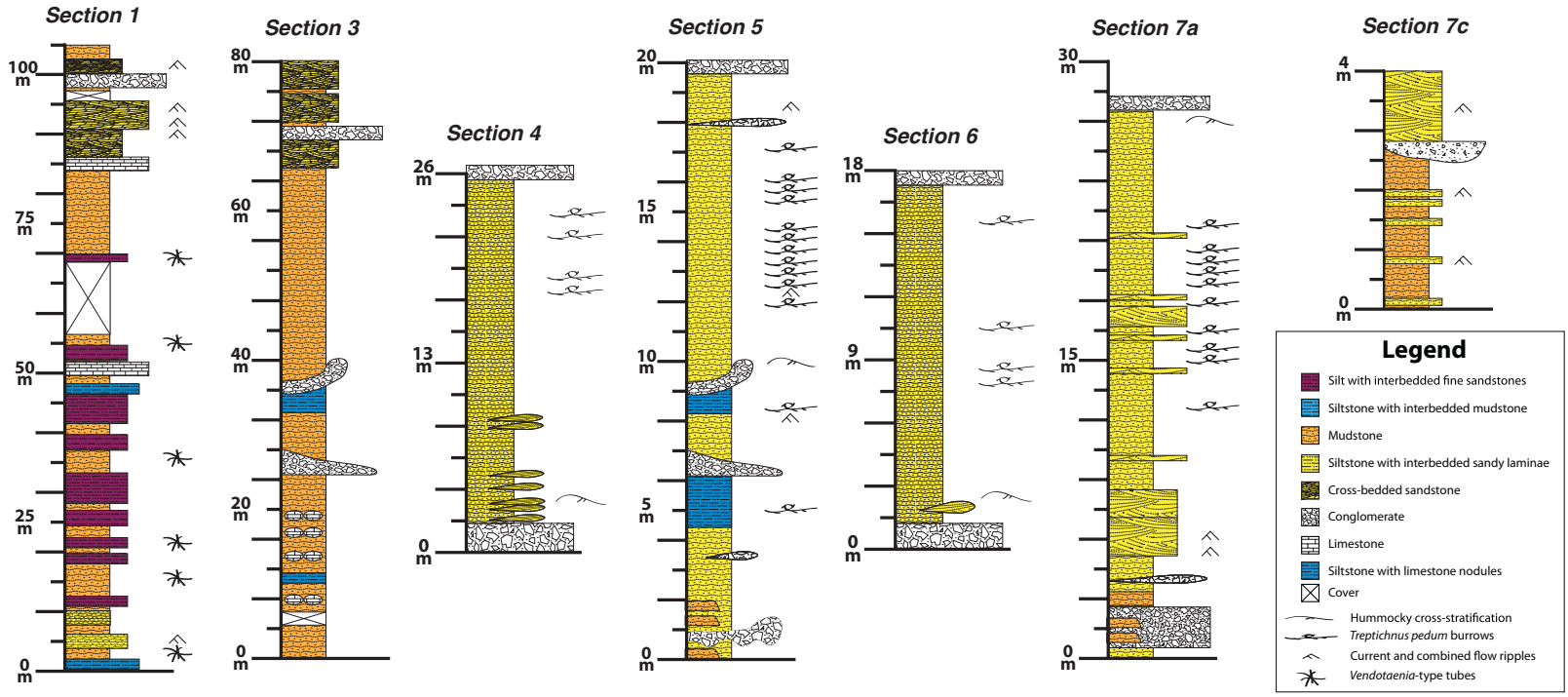


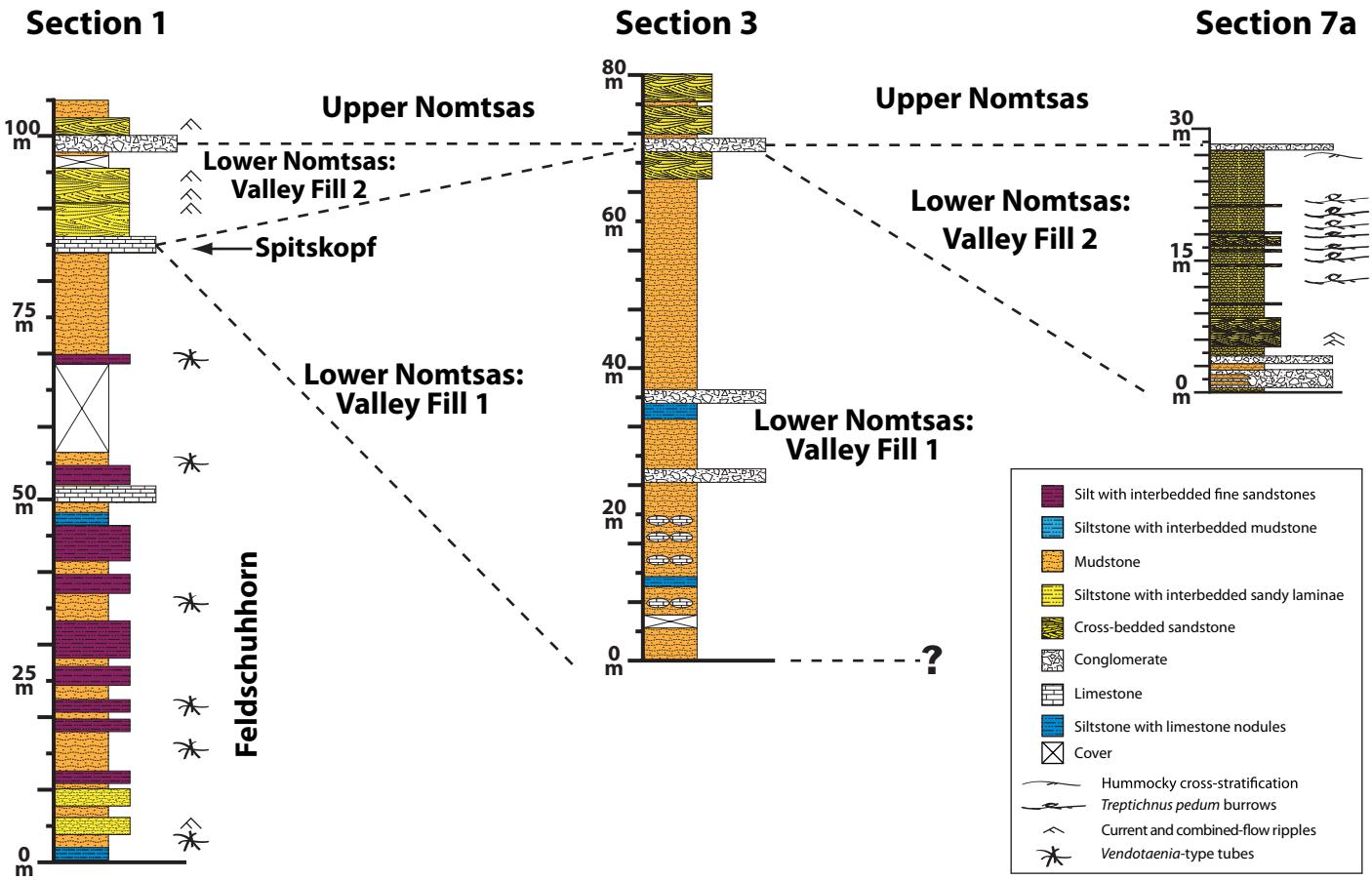

Base Upper Nomtsas
Base Valley Fill 2
Base Valley Fill 1
Upper Nomtsas Mbr.
Upper Nomtsas Mbr.
Valley Fill 2
Valley Fill 1
Valley Fill 1
Rotated Block
(Spitskopf)
Feldschuhhorn Mbr

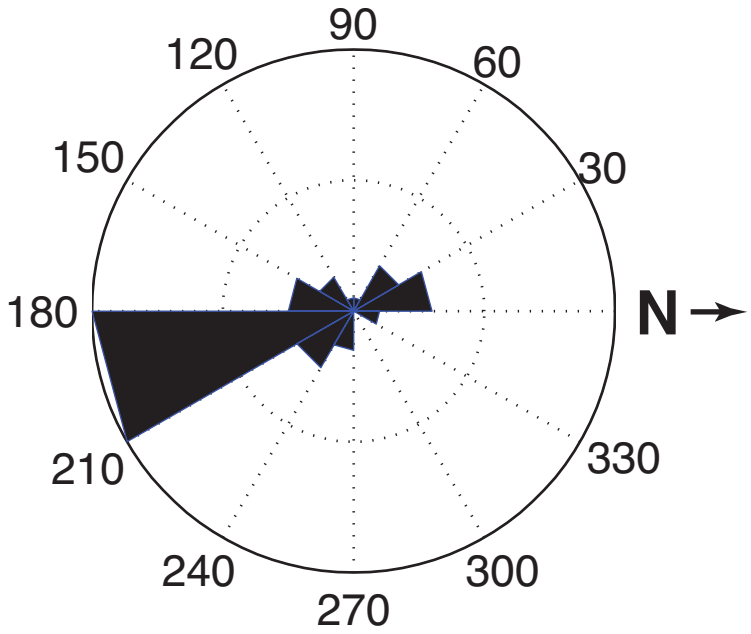

Base of Upper Nomtsas Mbr
Base of Valley Fill 1
Upper Nomtsas Mbr
Basal Spitskop
Valley Fill 1
Valley Fill 1
Feldschuhhorn Mbr

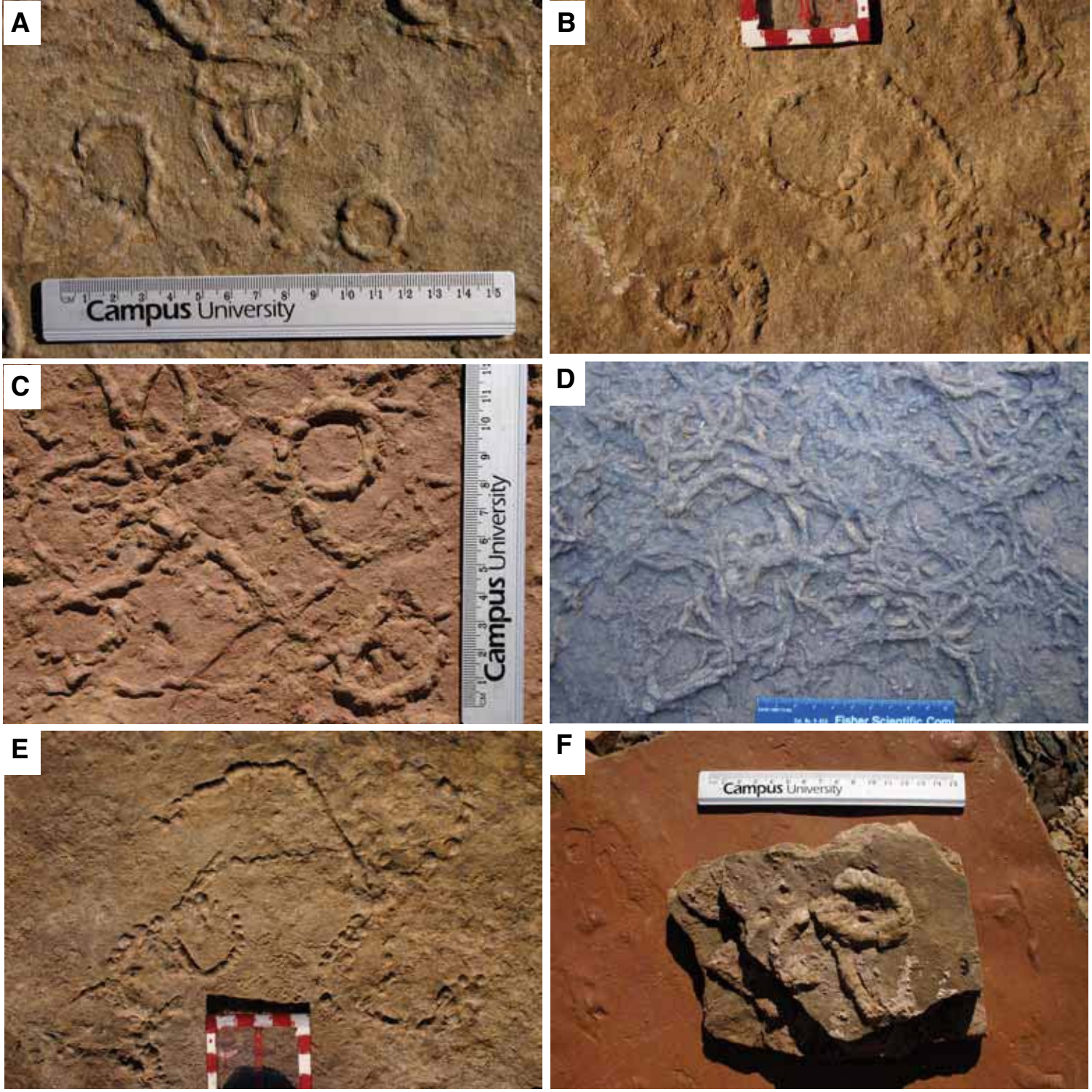

Upper Nomtsas Mbr
Valley Fill 2
Feldschuhhorn Mbr
Base of Upper Nomtsas Mbr
Base of Valley Fill 2


Upper Nomtsas Mbr
Valley Fill 2
Valley Fill 1
Feldschuhhorn Mbr
Base of Upper Nomtsas Mbr
Base of Valley Fill 2
Base of Valley Fill 1


Section 1
100 m
75 m
50 m
25 m
0 m
Section 3
80 m
60 m
40 m
20 m
0 m
Section 4
26 m
13 m
0 m
Section 5
20 m
15 m
10 m
5 m
0 m
Section 6
18 m
9 m
0 m
Section 7a
30 m
15 m
0 m
Section 7c
4 m
0 m
Legend
Silt with interbedded fine sandstones
Siltstone with interbedded mudstone
Mudstone
Siltstone with interbedded sandy laminae
Cross-bedded sandstone
Conglomerate
Limestone
Siltstone with limestone nodules
Cover
Hummocky cross-stratification
Treptichnus pedum burrows
Current and combined flow ripples
Vendotaenia-type tubes


Section 1
Section 3
Section 7a
Upper Nomtsas
Lower Nomtsas:
Valley Fill 2
Spitskopf
Lower Nomtsas:
Valley Fill 1
Feldschuhhorn
Upper Nomtsas
Lower Nomtsas:
Valley Fill 2
Lower Nomtsas:
Valley Fill 1
?
100 m
75 m
50 m
25 m
0 m
80 m
60 m
40 m
20 m
0 m
30 m
15 m
0 m
Silt with interbedded fine sandstones
Siltstone with interbedded mudstone
Mudstone
Siltstone with interbedded sandy laminae
Cross-bedded sandstone
Conglomerate
Limestone
Siltstone with limestone nodules
Cover
Hummocky cross-stratification
Treptichnus pedum burrows
Current and combined-flow ripples
Vendotaenia-type tubes


90
120
60
150
30
180
N
210
330
240
300
270


A
Campus University
B
C
Campus University
D
E
F
Campus University

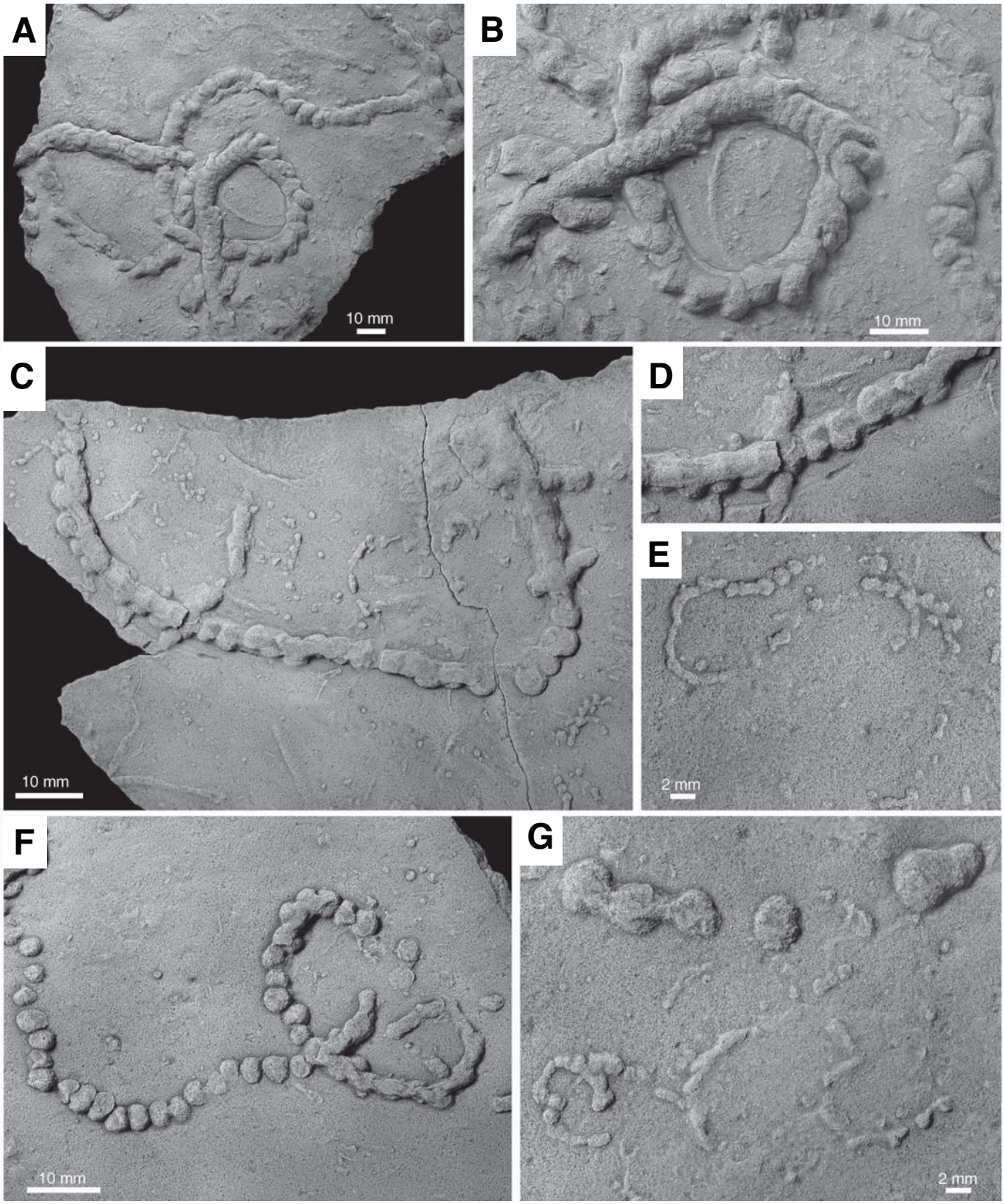

A
CM
1
2
3
4
Campus

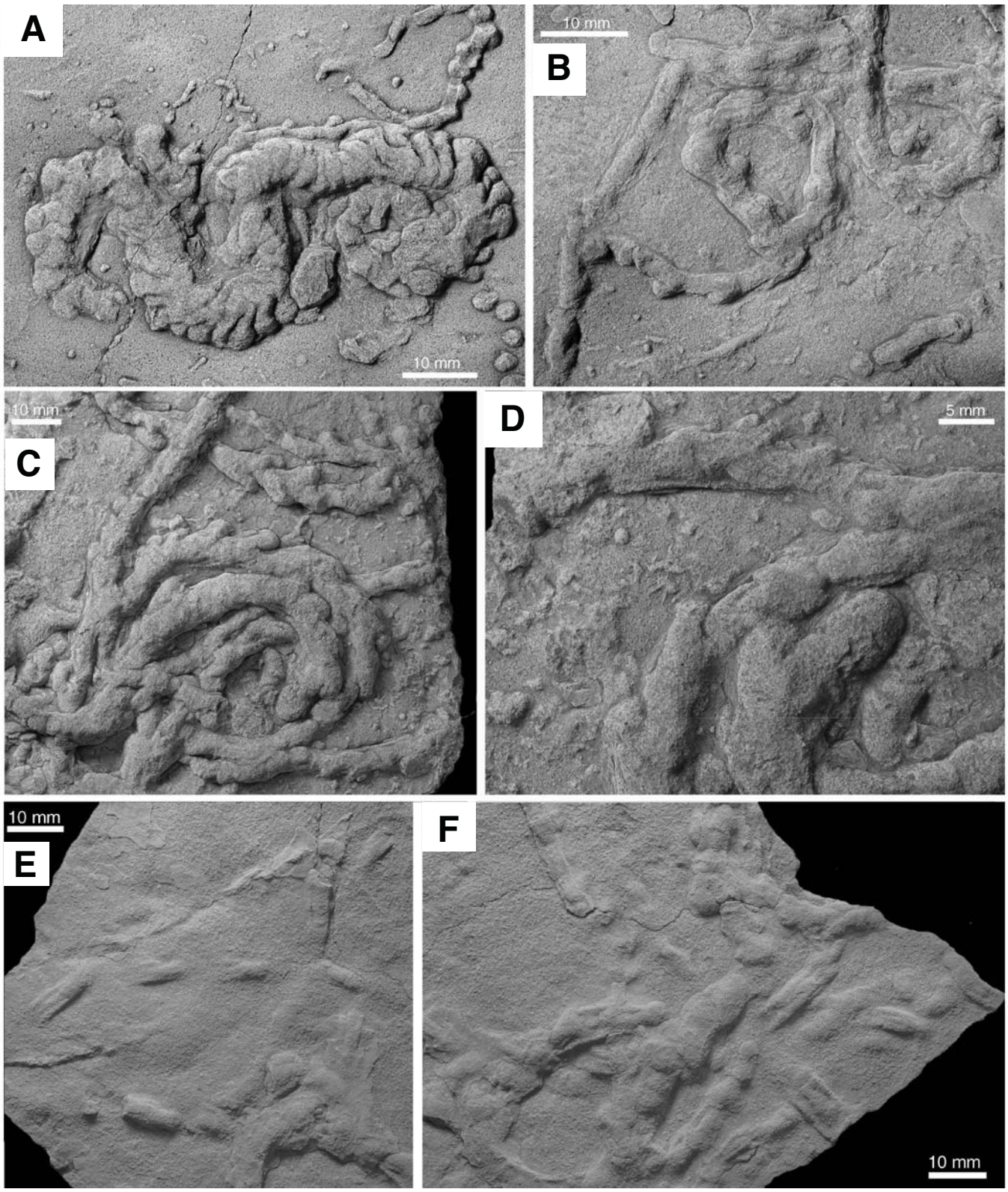

B
11
12
13
14
15

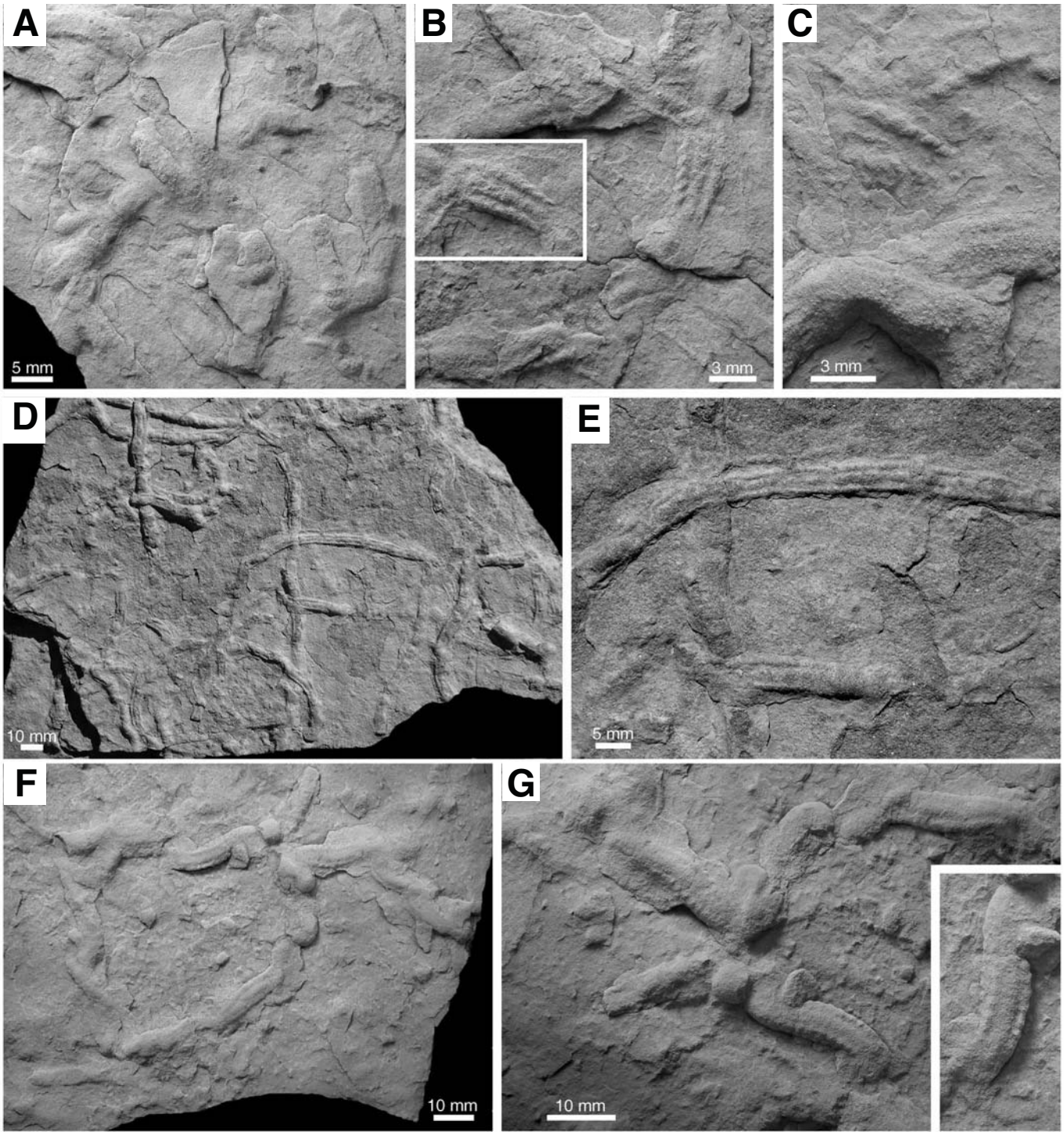

C

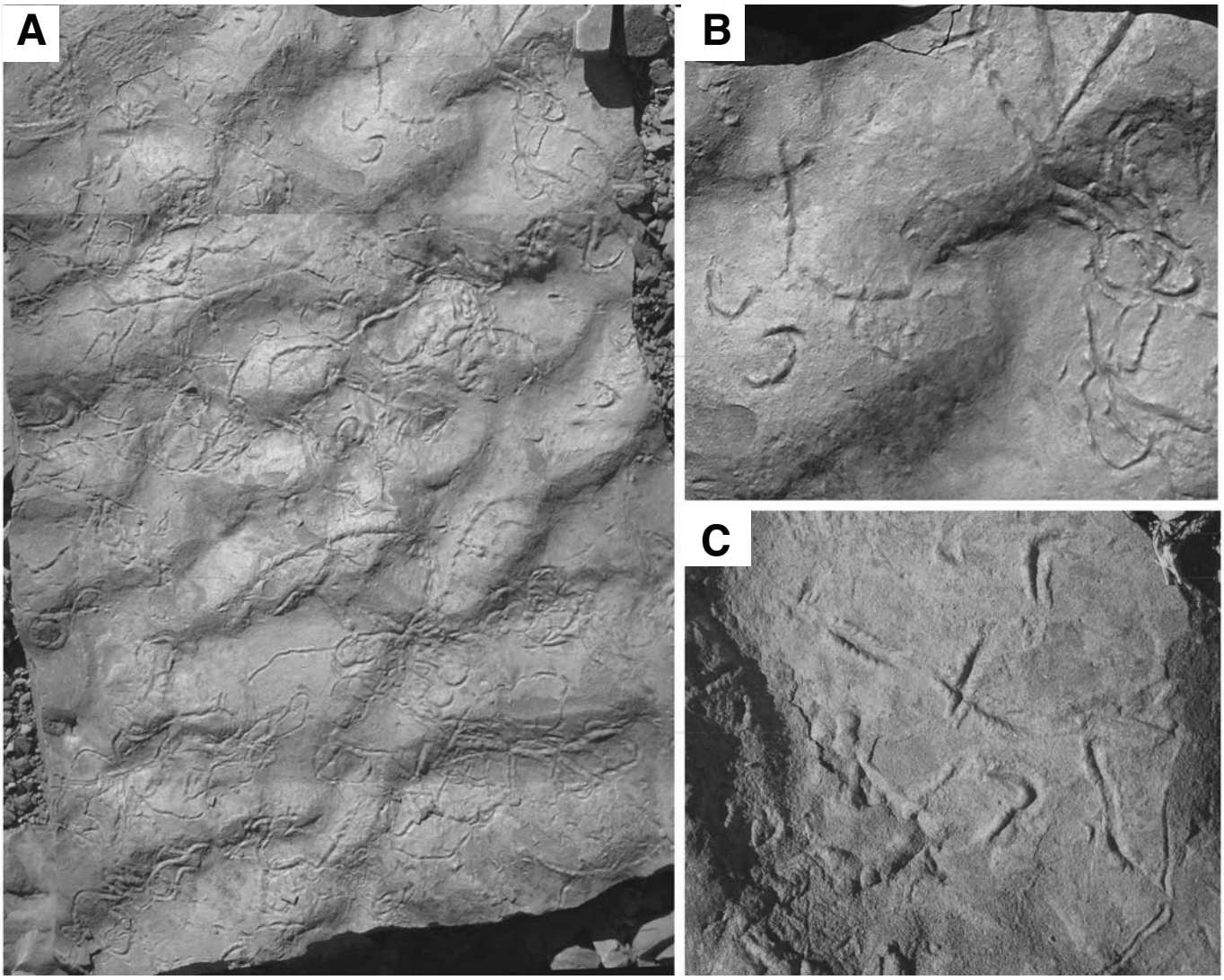

D
Campus University

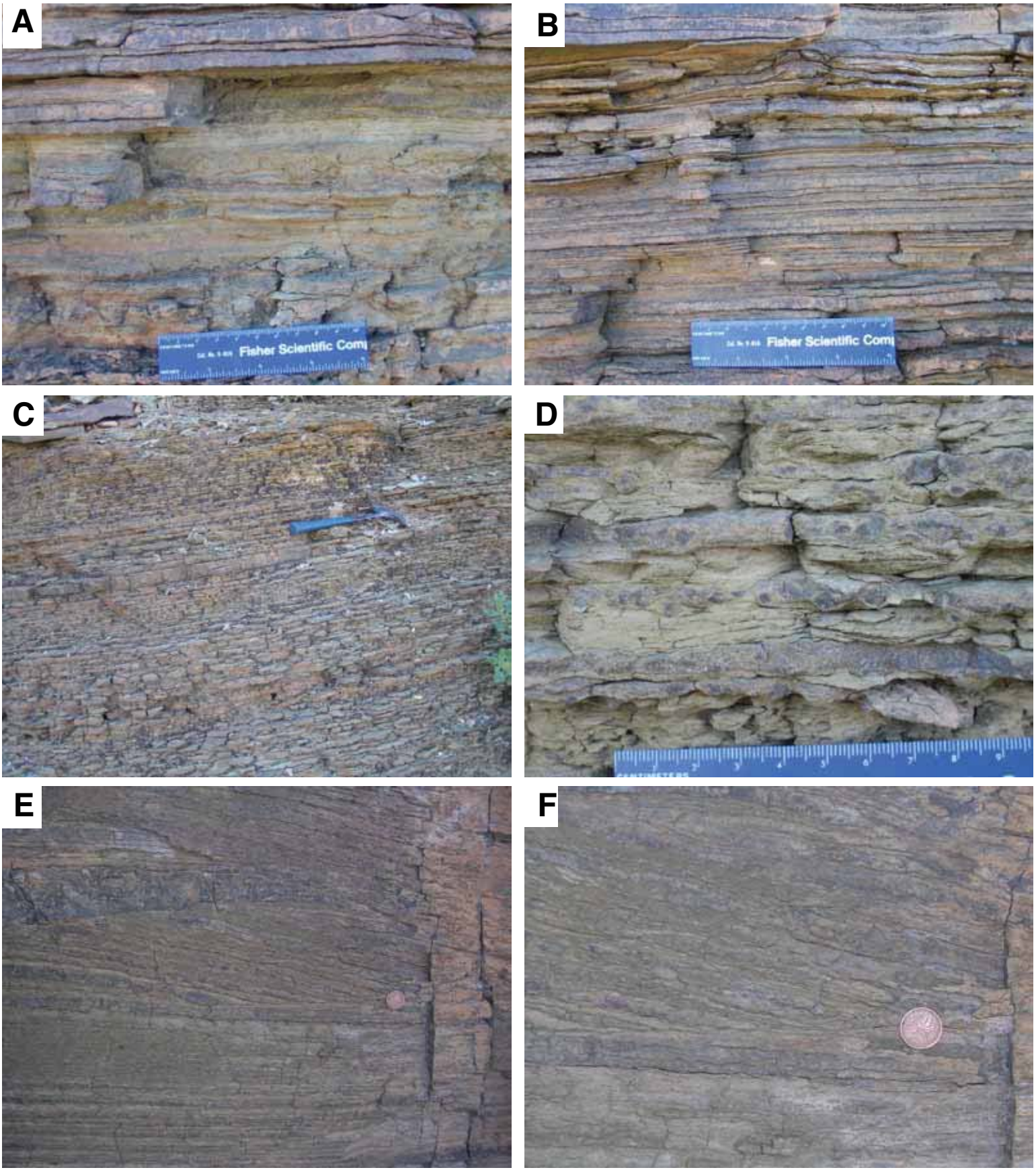

E
1
12
13
14
15

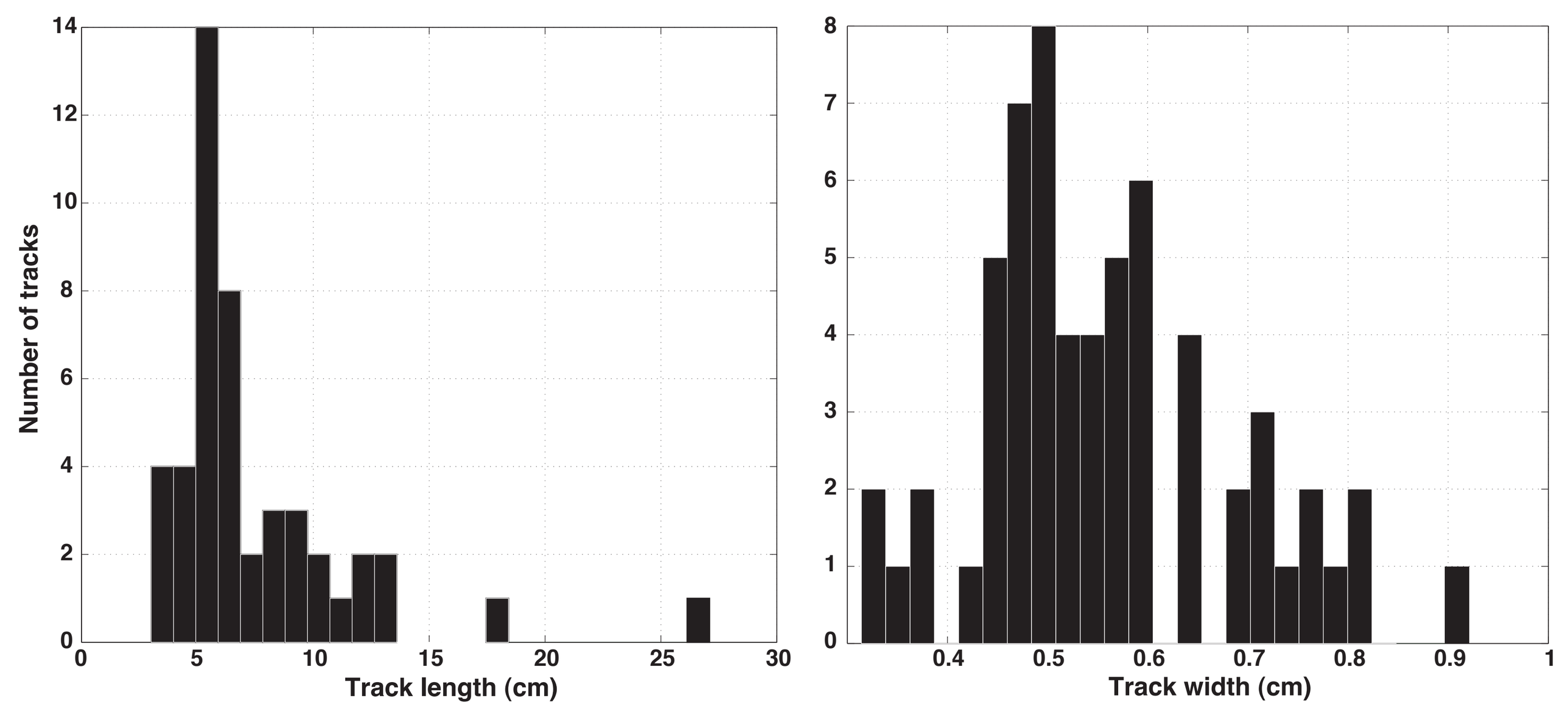

A
10 mm
B
10 mm
C
10 mm
D
E
2 mm
F
10 mm
G
2 mm

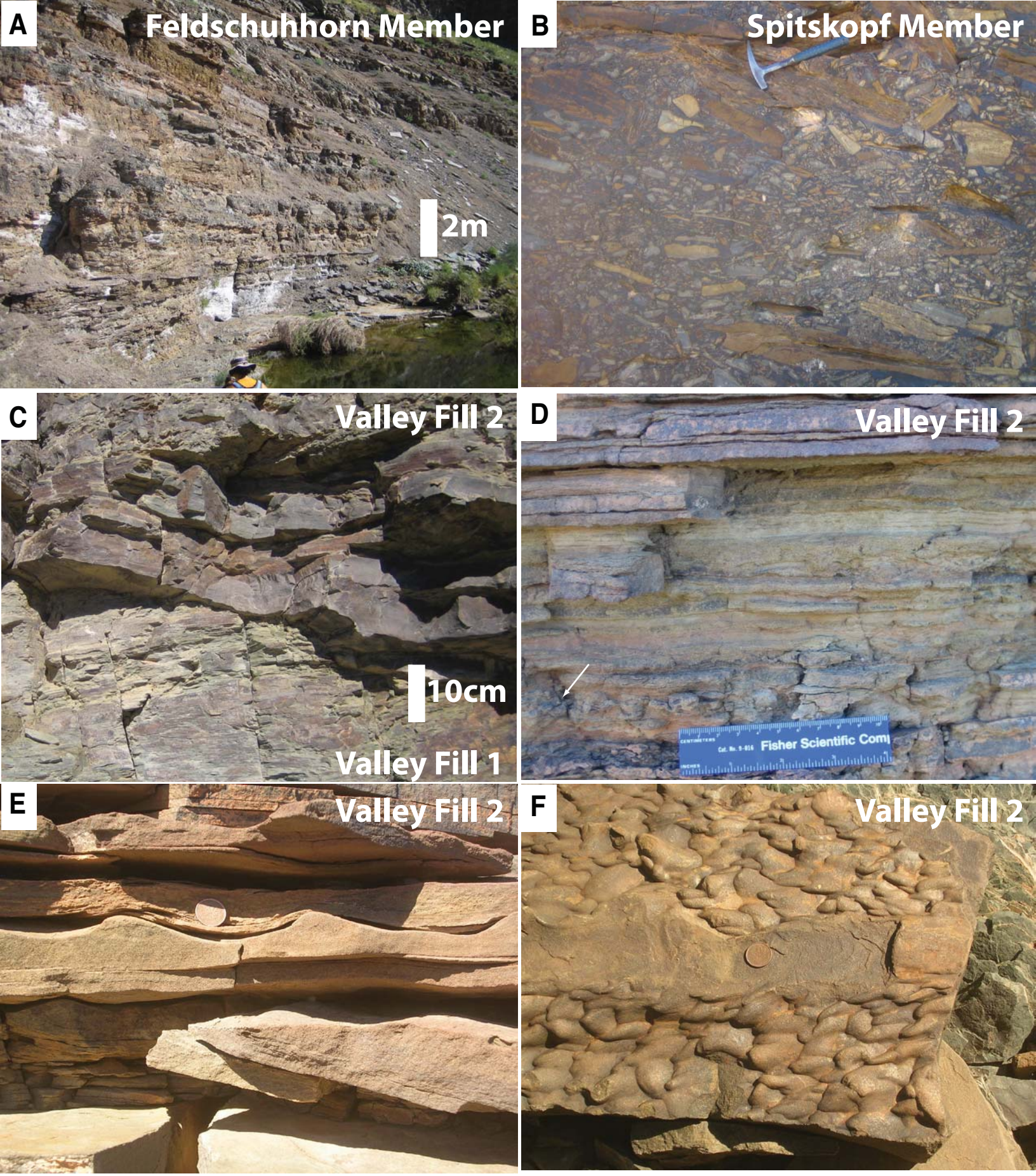

A
10 mm
B
10 mm
C
10 mm
D
5 mm
E
10 mm
F
10 mm


A
5 mm
B
3 mm
C
3 mm
D
10 mm
E
5 mm
F
10 mm
G
10 mm


A
B
C

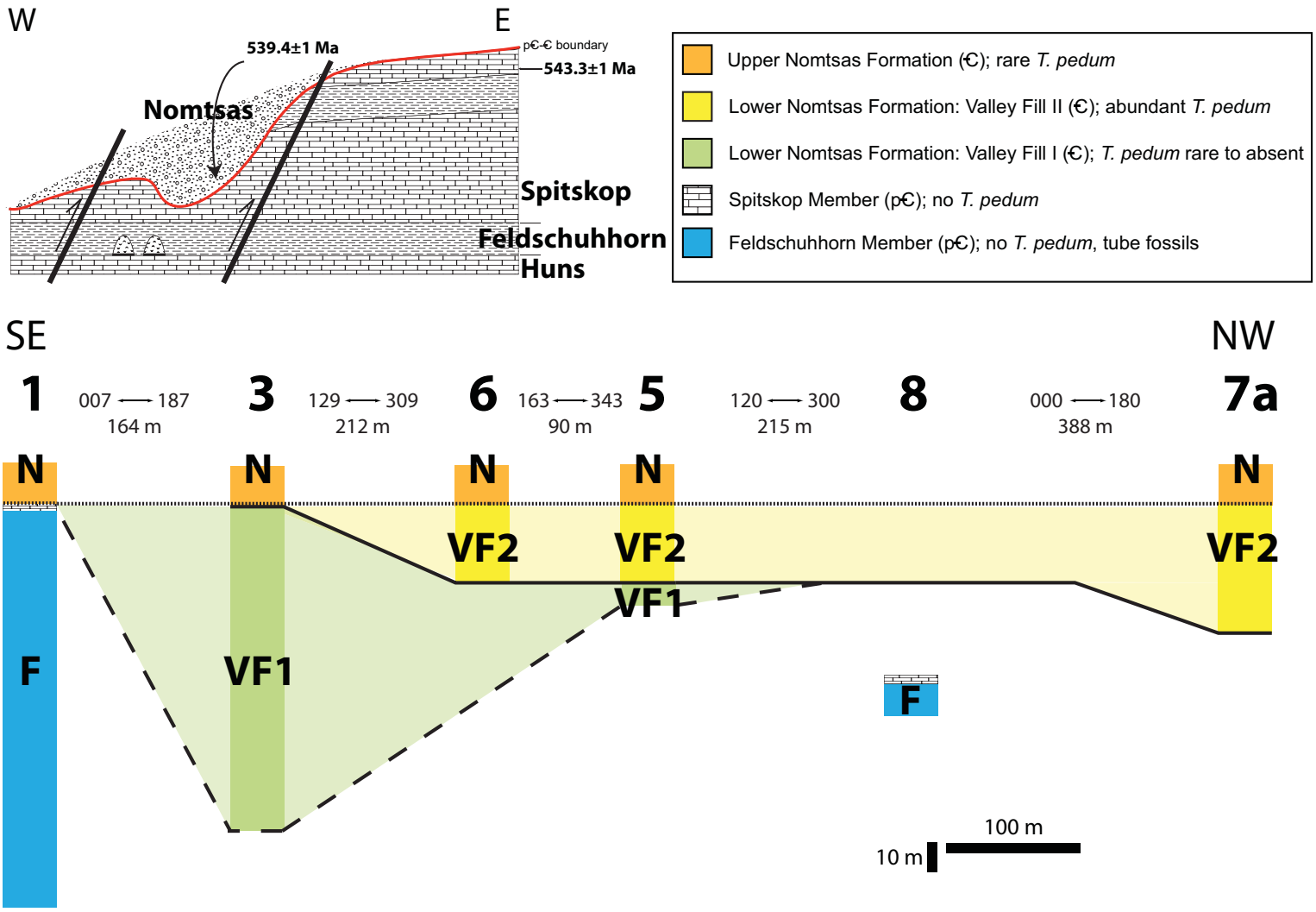

A
B
C
D
E
F

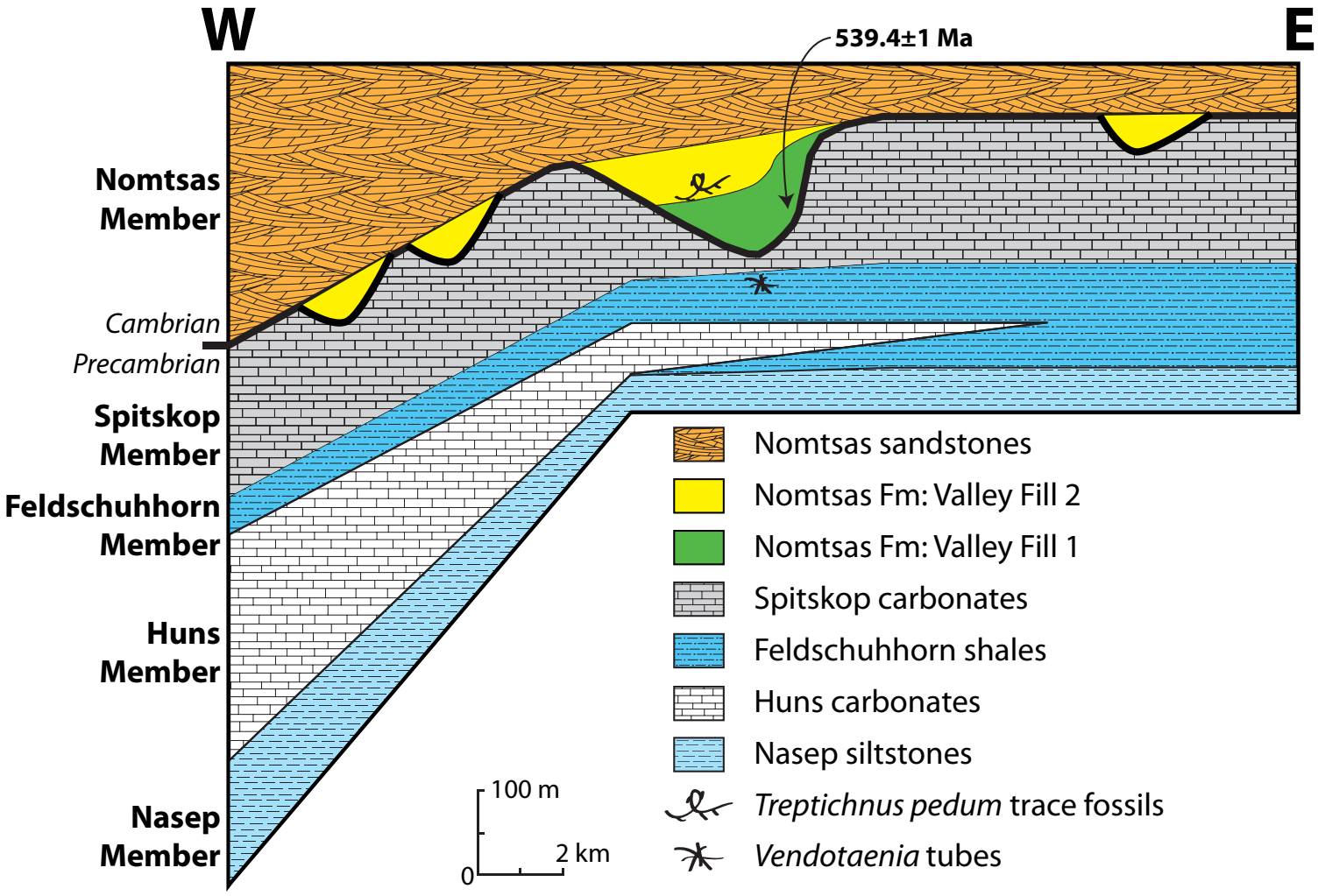

Number of tracks
Track length (cm)
Track width (cm)
0
2
4
6
8
10
12
14
0
5
10
15
20
25
30
1
2
3
4
5
6
7
8
0.4
0.5
0.6
0.7
0.8
0.9
1


A
Feldschuhhorn Member
2m
B
Spitskopf Member
C
Valley Fill 2
10cm
Valley Fill 1
D
Valley Fill 2
Fisher Scientific Com
E
Valley Fill 2
F
Valley Fill 2


A
2m


B


W
E
539.4±1 Ma
p€-€ boundary
543.3±1 Ma
Nomtsas
Spitskop
Feldschuhhorn
Huns
Upper Nomtsas Formation (€); rare T. pedum
Lower Nomtsas Formation: Valley Fill II (€); abundant T. pedum
Lower Nomtsas Formation: Valley Fill I (€); T. pedum rare to absent
Spitskop Member (p€); no T. pedum
Feldschuhhorn Member (p€); no T. pedum, tube fossils
SE
NW
1
007 ⟷ 187
164 m
3
129 ⟷ 309
212 m
6
163 ⟷ 343
90 m
5
120 ⟷ 300
215 m
8
000 ⟷ 180
388 m
7a
N
VF2
VF1
F
100 m
10 m


W
E
539.4±1 Ma
Nomtsas Member
Cambrian
Precambrian
Spitskop Member
Feldschuhhorn Member
Huns Member
Nasep Member
100 m
0
2 km
Nomtsas sandstones
Nomtsas Fm: Valley Fill 2
Nomtsas Fm: Valley Fill 1
Spitskop carbonates
Feldschuhhorn shales
Huns carbonates
Nasep siltstones
Treptichnus pedum trace fossils
Vendotaenia tubes